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# THE JOURNAL OF ECOLOGY

EDITED FOR THE  
BRITISH ECOLOGICAL SOCIETY

BY  
A. G. TANSLEY

VOLUME XXIV  
1936

WITH TWENTY-THREE PLATES, AND NUMEROUS  
FIGURES IN THE TEXT



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## CORRIGENDA. VOL. XXIV

P. W. RICHARDS. "Ecological Observations on the Rain Forest of Mount Dulit, Sarawak, Part I."

- p. 21, last paragraph: the percentages of Dipterocarpaceae are given wrongly: *for* "17 per cent. of trees over 8 in. diameter and 44 per cent. of those over 16 in." *read* "15.7 per cent. of trees over 8 in. diameter and 46.8 per cent. of those over 16 in."
- p. 22, 11th line from bottom of page: *after* "Jack" *delete* "!"
- p. 30, first paragraph, line 3: *for* "ten" *read* "fourteen": line 9: *for* "*Orat matah* and *Resak sabut*, both Dipterocarps" *read* "*Orat matah* (Dipterocarpaceae), *Resak sabut*"
- p. 30, fourth paragraph, line 5: the percentages of Dipterocarpaceae at Marudi are given wrongly: *for* "40.5 and 51.3 respectively" *read* "36.9 and 46.2 respectively"
- p. 31, sixth paragraph, line 7: *for* "*Polygala venenox* Juss. ex Poir. sp." *read* "*Polygala venenosa* Juss. ex Poir."

J. G. MYERS. "Savannah and Forest Vegetation of the Interior Guiana Plateau."

- p. 184, lines 13 to 16 should read: "Such dews are unknown in open savannah of the Rupununi. The soil is generally sandy. I saw none of the perdigon or pebbly areas so frequent in the Rupununi savannahs."

# ECOLOGICAL OBSERVATIONS ON THE RAIN FOREST OF MOUNT DULIT, SARAWAK. PART I

By P. W. RICHARDS

(With Plates I—III and six Figures in the Text)

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## I. INTRODUCTION

THE ecological work described in the following paper was carried out from August to December 1932, when the author was a member of the Oxford University Expedition to Sarawak. A general account of the work of the Expedition has been given by T. H. Harrisson (1933).

The chief aim of the ecological survey was to collect data for a detailed comparison of a typical area of rain forest in the eastern tropics with the area in British Guiana, which had previously been studied by T. A. W. Davis and the present writer (1933, 1934).

A large collection of plants was made in the Dulit neighbourhood by P. M. Syngé and the author: the first set has been presented to the Kew herbarium. In the following account collector's numbers (S. = Syngé, R. = Richards) have been quoted in most cases. The author has to thank the fol-



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lowing experts for naming the species mentioned in this paper: Mr F. Ballard of Kew (*Lycopodium*), Mr C. E. Carr (orchids), Prof. B. H. Danser of Groningen (Loranthaceae and Nepenthaceae), Mr H. N. Dixon of Northampton (mosses), Mr R. E. Holttum of Singapore Botanic Garden (ferns), Mr C. E. Hubbard of Kew (grasses), Dr J. Hutchinson of Kew (*Rhododendron*), Mr A. B. Jackson (gymnosperms), Miss J. T. Koster of Leiden (*Vernonia*), Mr H. K. Airy-Shaw of Kew (Ericaceae, Rubiaceae, etc.), Dr C. G. G. J. van Steenis of Buitenzorg (saprophytes, etc.), Mr C. F. Symington of the F.M.S. Forestry Research Institute (Dipterocarpaceae), Dr H. Uttien of Utrecht (Cyperaceae) and Mr E. F. Warburg of Cambridge (Fagaceae). The identification of all plants for which actual specific names are given rests on specimens named by these authorities, except where no collector's number is quoted, in which case they rest on the writer's own authority alone. Taxonomic papers on the Cyperaceae (Uttien, 1935), Dipterocarpaceae (Symington, 1934), Ericaceae (Airy-Shaw, 1935), Orchidaceae (Carr, 1934), Loranthaceae (Danser, 1934) and mosses (Dixon, 1935) have already been published, and papers on other groups are in preparation.

The author's thanks are also due to a member of the staff of Sarawak Oilfields, Ltd., for information on the geology of Mt Dulit, to Mr P. M. Synge for taking the photographs, and to Dr C. G. G. J. van Steenis for preparing for him a list of papers on the vegetation of Netherlands India.

Some further notes on the ecology of the bryophytes will be found in the taxonomic paper on the mosses (Dixon, 1935).

### II. GENERAL FEATURES OF THE DISTRICT

The *raj* of Sarawak forms the north-western part of the island of Borneo and lies between approximately 1 and 5° N. lat. The district with which this paper is chiefly concerned lies in its northern part (4th Division), in the basins of the rivers Baram and Rejang.

The Base Camp of the Oxford Expedition (lat. 3° 19' N., long. 114° 17' E.) was situated near the native village of Long Kapah on the left bank of the Tinjar, the chief tributary of the Baram, and was about 98 km. (in a direct line) from the coast. The Tinjar valley at this point is rather narrow. About 4 km. to the south-west is the crest of Mt Dulit, an escarpment of Lower Miocene sandstone which runs more or less parallel to the general course of the river for some 50 km., forming a ridge of very even height: the lowest points are probably never less than 1100 m. high and the highest not much more than 1400 m.<sup>1</sup> At its eastern end Mt Dulit is joined to the mountain backbone of Borneo by a saddle about 600 m. high. The slope facing the Tinjar is very steep, and in many places there are overhanging cliffs of perhaps 60 m.: it is drained by innumerable torrential streams, some of which are

<sup>1</sup> The highest peak climbed by members of the Expedition, Igok Peak, was 1403 m. (4600 ft.) high, but this is not the highest point on the ridge (cf. **Harrison**, 1933).

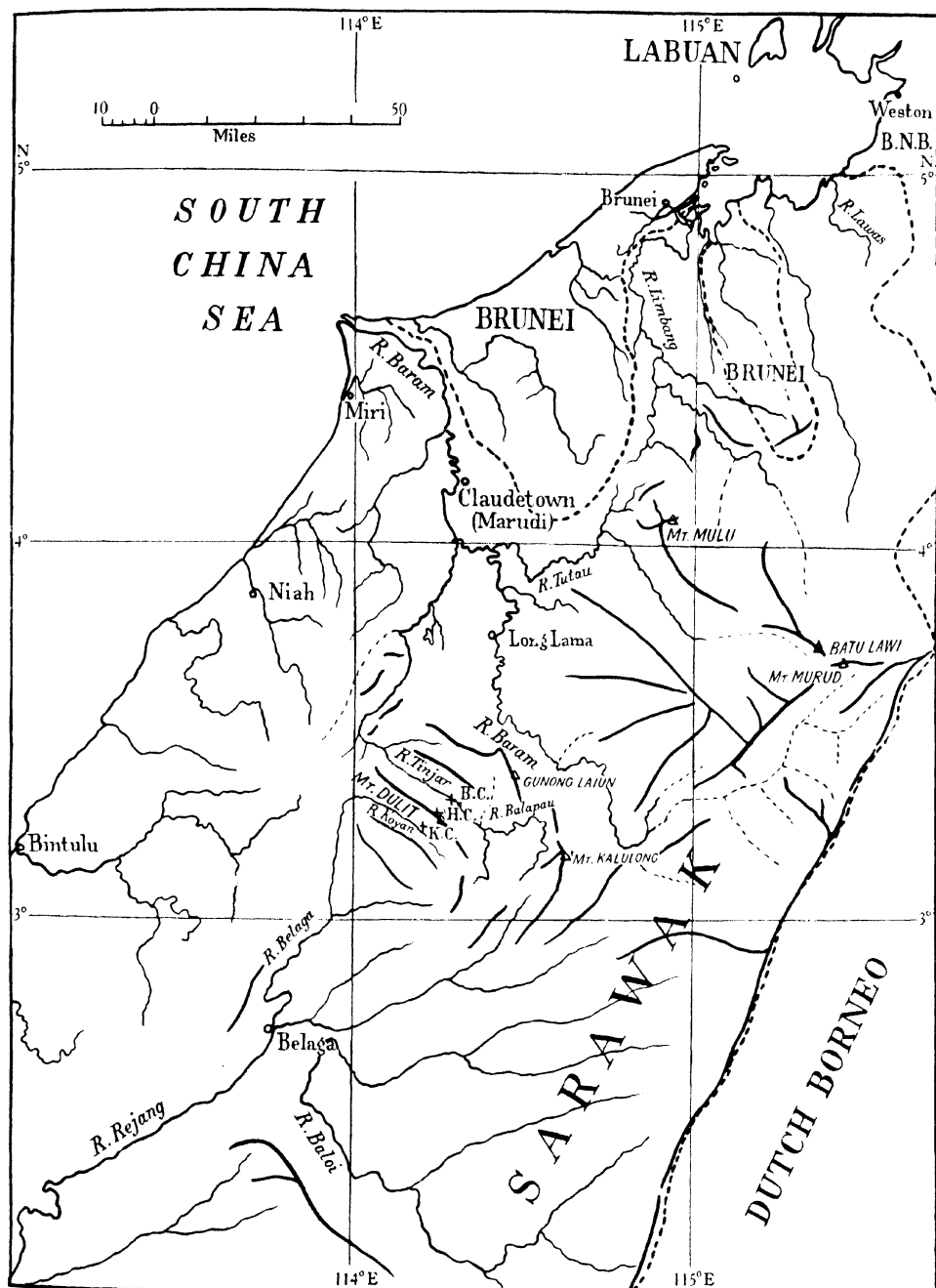


FIG. 1. Map of northern Sarawak. Based on Government surveys and observations made by the Oxford Expedition. B.C. = Base Camp, H.C. = High Camp, K.C. = Koyan Camp.

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interrupted by high waterfalls. The south-western side of the mountain slopes down more gently to the valley of the Koyan, a small river running into the Belaga and thence into the Rejang.

To the north of the Tinjar there are some high ridges forming the watershed between it and the Baram. They seem to be formed mainly of shales, which, like the Dulit sandstone, are of Lower Miocene age. The highest peak on this watershed is Mt Laiun, estimated to be about 1100 m. high. Between these ridges and the Tinjar and between it and the Dulit escarpment there is a network of steep-sided spurs, mostly under 300 m. high. There is only a narrow flood-plain.

The population of the district consists of settled aboriginal tribes (Sebops and other "Klemantans", Kenyahs) and a few bands of nomads (Punans) in the forests. The native long houses (villages sometimes of over 500 inhabitants) are situated on the river banks and are about 10-15 km. apart on the average.

The staple industry of the settled peoples is the cultivation of hill rice (not irrigated). A field is used for a few years only and is then allowed to develop into second-growth forest. New fields are made by felling and burning either virgin or old secondary forest (Pl. I, phot. 1). As a result of this wasteful method of cultivation and the comparative scarcity of suitable ground, it is not surprising that there is no virgin forest left on the flood-plain of the Tinjar or on the gentler slopes adjoining it.

The natives collect dammar (resin of *Agathis*), jelutong (latex of *Dyera* spp.), rotans and other products from the forest. They also cut down a certain number of trees for their own use, but there is no systematic exploitation of the timber.

Besides the Base Camp, the Oxford Expedition built a camp on the crest of the Dulit escarpment about 4 km. south-west of the Base Camp ("High Camp", alt. 1230 m. above sea-level). The areas which were studied ecologically were the primary forest on the low ridges near the Base Camp and on the north face of Dulit near the path connecting the two camps, the Dulit ridge for several kilometres on each side of the High Camp, the Koyan valley at the nearest point to the High Camp, and the south-western slopes of Dulit between the two. A short excursion for reconnaissance and collecting purposes was made to the summit of Gunong Laiun, through the valley of the Balapau, a small tributary which joins the Tinjar about 9 km. above the Base Camp.

#### III. TYPES OF VEGETATION

The natural climax vegetation of the whole of the Dulit district, as of nearly the whole of Borneo, except the summits of the highest mountains, is evergreen rain forest.

The primary forest (*hutan tua* of the Malays) of the Dulit district was not homogeneous but belongs to three main types:

(i) *The Mixed forest on heavy clay and loam.* This was the only type of primary forest met with in the Tinjar valley below about 1150 m. A very



Phot. 1. Natives preparing a field for hill rice, Tinjar valley. Secondary forest in background.



Phot. 2. Mixed forest on lower slopes of Mt. Dulit (alt. c. 300-400 m.) seen from half way mountain. Note the non-continuous first storey.



small patch of it was seen in the Koyan valley. It represents what is usually understood by "typical tropical rain forest".

(ii) *The "Heath forest" of sandy soils.* Most of the forest examined in the Koyan valley was of this type. It lives under similar climatic conditions to the Mixed forest and resembles it in structure, but differs widely from it in floristic composition; it is probably best regarded as an edaphic climax type.

(iii) *The Montane rain forest or "Moss forest".* This is found on the mountains above about 1150 m. and therefore under very different climatic conditions to (i) and (ii). It is no doubt a climatic climax, and in both its structure and floristic composition it is so different from the lowland forest that there is no justification for speaking of it as "tropical rain forest".

As has been mentioned, one of the chief objects in studying the vegetation of Mt Dulit was to compare the forest types with those of the Moraballi Creek area in British Guiana.

Because both are climax types and both are found on fairly similar soils, it will be natural to compare the Dulit Mixed forest with the Mixed forest of Guiana. Though they have no species of vascular plants in common, there is a considerable agreement in structure between the two, as will be seen later. Since the Sarawak "Heath forest" grows on white sand, it might be expected to show some analogies with the Wallaba forest of Guiana: actually these analogies are found to be surprisingly numerous and far-reaching.

As all the Moraballi Creek area was under 100 m. above sea-level, there was, of course, no type of forest comparable with the Montane rain forest of Dulit.

Besides the primary or virgin forest, there were large areas of secondary forest of various ages, all or most of which were formerly cultivated. This secondary forest is called by the Malays *jerameh* (Brunei dialect) or *belukar*. Apart from its very characteristic general aspect, secondary forest can be recognised by the following features:

(i) The scarcity of very large trees. They are not necessarily quite absent, as the natives when making *padi* (rice) fields often leave a few exceptionally large trees, e.g. large specimens of *Tapang* (*Koompassia* sp.?) unfelled. If large trees are present, there is a marked absence of sizes intermediate between them and the average-sized canopy trees.

(ii) The numerous small openings and the general irregularity of structure.

(iii) The abundance of lianes: these nearly always make it troublesome to walk through secondary forest without cutting a path, though that is seldom difficult in old forest.

(iv) The presence of certain indicator species. It would need much further work to give a list of these, but probably most species of *Macaranga* and some other Euphorbiaceae (small trees), *Curculigo* spp. (herbs), and a palm (probably *Arenga undulatifolia* Becc.) are indicators of secondary forest. Since, however,

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most of the characteristic secondary forest species also occur in the "holes" in primary forest produced by the death of large canopy trees, it is only the abundance of an indicator over a considerable area which is diagnostic. Conversely, there are no doubt many species which are probably indicators of primary forest, e.g. many of the Dipterocarpaceae and some of the ground herbs.

Seen from the Dulit ridge (nearly 1200 m. above) the primary and secondary forest in the Tinjar valley can easily be distinguished and are divided by a sharp line. The primary forest is dull green and the crowns of individual trees in it can be distinguished at great distances, perhaps 10–15 km. (cf. Pl. I, phot. 2): the secondary forest is bright green and, even close at hand, looks like a smooth lawn.

The soil of the secondary forest is always red clay or loam, and the original vegetation was no doubt forest of the Mixed type, except perhaps on land liable to flooding, where there were indications that some type of swamp forest may formerly have existed.

Owing to lack of time very little attention was given to the ecology of the secondary forest, so the present account will deal only with the primary forest.

### **Lowland rain forest**

#### (1) CLIMATE

The nearest meteorological stations to the Oxford Expedition's Base Camp at which full observations are made are Miri and Bintulu, both on the coast about 160 km. away. It will therefore be impossible to give a very definite picture of the climate of the Dulit district. Since, however, variations in meteorological conditions from season to season and from year to year are relatively slight in Sarawak, some indications of its general character can be obtained from such observations as it was possible to make during the course of the expedition.

Owing to interruptions due to other work and the absence of trustworthy assistance, it was impossible to carry on continuous observations over the whole period of the expedition (August to November). Damp and insects also caused occasional trouble with the recording instruments, so that some days' observations had to be discarded. Some observations were made actually in primary forest, as well as at the Base Camp (open clearing on river bank, altitude under 100 m. above sea-level): these will be discussed later (p. 17).

Sarawak has a typically equatorial climate. The temperature is high, with only very slight seasonal variations (mean about 27° C.). The annual rainfall varies from 287 cm. at Sibu to 465 cm. at Mattang,<sup>1</sup> and is well distributed through the year; at none of the recording stations is the average rainfall for any month less than 10 cm.<sup>1</sup> The north-east monsoon blows from about the

<sup>1</sup> Averages for 1920–5 from "Rainfall in Sarawak" (1933).

beginning of November till March or April, and in the southern part of the country there is a marked maximum of rainfall during that period, but in the north (5th Division) distinct wet and dry seasons are not recognisable. In some districts there may occasionally be no rain for periods of as much as three weeks, but longer droughts are unknown.

The following is a summary of the observations of *temperature* at the Mt Dulit Base Camp:

	° C.		Date
Absolute maximum, Sept. 1st to Nov. 19th	33		Sept. 19th
Absolute minimum, Sept. 1st to Nov. 19th	22		Nov. 3rd
	September ° C.	October ° C.	November ° C.
Mean maximum	31	28	29
Mean minimum	23	23	23
Mean	27	26	26
Range of maximum	5	4	3
Range of minimum	2	2	2
Greatest daily range	9	8	8
Mean daily range	8	6	6
Number of days observed	18	16	20

The course of the temperature curve varied very little from day to day. The maximum was usually reached in the afternoon (about 4 p.m.). The minimum was generally about sunrise (6 a.m.), but often the temperature stayed constant at or near the minimum from midnight or earlier till 7 or 8 a.m.

The annual *rainfall* at the Mt Dulit Base Camp is presumably much heavier than at the nearest recording station, Miri (292 cm.), which is situated on a low-lying coast, and may well be of the order of 450 cm.

During the whole period of the expedition there were never more than four consecutive days without rain. As far as our own experience goes, most of the rainfall is in the form of heavy thunder showers usually after 5 p.m. There were no whole days of continuous rain, but after the change of monsoon at the end of October there were often several showers in the morning and afternoon as well as the usual evening downpour.

*Winds* were usually light, but strong gusts lasting a few minutes often blew up stream just before rain. These gusts seemed to be felt only in the immediate neighbourhood of the river. Away from it strong wind was apparently very rare.

Records of *relative humidity* were made from October 13th to 22nd by means of a hair hygrograph checked every day against a whirling wet- and dry-bulb thermometer. All the curves are very similar. All night the humidity remains constant at saturation or a few per cent. below. It begins to fall at sunrise, or very soon after, and reaches a minimum at about 2 p.m. (nearly 2 hours earlier than the maximum of temperature). The night level is reached at sunset or earlier, according to the rainfall conditions. The oscillations superimposed on the general course of the curve during the daytime are small.



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The mean minimum humidity for the 10 days was 61 per cent., which is equivalent to a saturation deficit of about 12 mm.

*Sunshine* records show a mean duration of 3 hr. 30 min. in October (13 days' observations) and 2 hr. 55 min. in November (19 days' observations). Both figures are probably far below the yearly average. The maximum daily duration during these months was 6 hr. 55 min.

From the general character of the climate little periodicity is to be expected in the vegetation. Very little information could be obtained as to flowering seasons, but a Malay forest guard said that the Dipterocarpaceae (the most important family of first- and second-storey trees) had definite seasons when many individuals of different species were in flower together, but that they occurred at irregular intervals which were sometimes longer than a year. As there had been one such season about 3 months before our arrival at Mt Dulit, it was impossible to get material for identification of most of the members of this family. Individuals of undergrowth trees, shrubs and herbs could be found in flower at any time during our stay (August to November).

A large number of trees shed all their leaves and simultaneously produced a new set of leaves without ever becoming completely bare, e.g. some Dipterocarpaceae and Rengas (Anacardiaceae). In a few cases there was a delay in producing the new foliage, so that the tree was quite bare for a few weeks; this condition was noticed in the Tapang (*Koompassia* sp.?, Leguminosae) and in a number of unidentified species. A large proportion of the trees acquired new foliage in mid-October, just before the change of monsoon.

### (2) MIXED FOREST

#### (i) *Habitat and soil conditions*

This type of forest covers a much larger proportion of the district than either of the other two types, and though it varies in character from place to place on a small scale, it is very uniform on the whole.

The country where it is found consists of a complicated system of narrow ridges, drained by many small and rapid streamlets with rocky beds. Some of the ridges lead up gradually to the main ranges, others are independent and are separated from the main ranges by low *cols*. Their summits are seldom more than a few metres wide, and the sides are so steep that were they not covered with trees they would often be difficult to climb, especially as the clayey soil becomes exceedingly slippery when wet. Large rocks and boulders are frequent, especially on the higher ridges and near the main mountain ranges.

The floor of the forest is covered with a layer of dead leaves usually not more than 2 cm. thick. On the ridge sides it does not always cover the whole surface, so that patches of bare soil can be seen. On level ridge summits it is somewhat thicker and in hollows may accumulate to a depth of perhaps 1 dm.

The soil is everywhere very uniform in type. It is a heavy and usually

very sticky bright yellow loam, sometimes, but not always, containing hard reddish concretions. It has not been determined whether this soil is lateritic or a true laterite, as defined by Martin and Doyne.<sup>1</sup> Only the top few centimetres are stained with humus.

The following soil profiles were examined:

I. Side of narrow ridge, right bank of Tinjar,<sup>2</sup> altitude under 300 m. Thin layer of dead leaves imperfectly covering surface. (27)<sup>3</sup> 0–10 cm.: yellow loam, tinged slightly grey with humus, passing insensibly into the underlying layer. (28) 10–74 cm.: pure yellow loam with small greyish patches.

II. Summit of same ridge as I,<sup>2</sup> altitude under 300 m. Continuous, rather well-rotted layer of dead leaves on surface. (29) 0–3 cm.: brownish grey loam. (30) 3–62 cm.: yellow, friable, but slightly sticky, loam containing hard concretions which became more and more numerous till at 62 cm. further digging is very difficult.

III. Crest of broad buttress ridge of Mt Dulit, altitude 450 m. Soil surface covered with continuous layer of dead leaves. (31) 0–30 cm.: bright yellow, very sticky, loam, slightly crumbly; topmost 2 cm. with faint humus stain. (32) 30–64 cm.: bright yellow, very sticky loam.

The analysis<sup>4</sup> of the soil samples gave the following results:

*Soil samples, Mixed forest*

Profile	No. of sample	Depth cm.	Comber colour	pH	Organic matter %	Moisture at "sticky point" %	Percentage of sand (1.0– 0.04 mm.)	Index of texture
I	27	0–10	Red	4.7	7.36	33.4	37.3	26
	28	10–74	Pale red on standing	4.9	1.11	30.3	36.0	23
II	29	0–3	Red	4.5	2.70	32.4	55.5	21
	30	3–62	Pale red on standing	4.6	0.82	30.2	58.8	18
III	31	0–30	Red	4.4	4.24	31.5	56.0	20
	32	30–64	Pale pinkish on standing	4.9	0.87	32.0	24.3	27

The concretions in sample 30 were broken up and not counted as a gravel fraction.

The shallowness and lighter texture of the soil of the summit as compared with the side of the same ridge may be noted.

(ii) *Structure*

The plants which form the Mixed forest may be grouped as follows, according to their methods of solving the light problem:

A. Autotrophic.

- (1) Plants not dependent on others for mechanical support (trees, shrubs and herbs).

<sup>1</sup> These authors propose to restrict the term lateritic to soils where the silica-alumina ratio is less than 2.0 and the term true laterite to those where it is less than 1.33 (Martin and Doyne, 1927).

<sup>2</sup> These profiles were dug close to the clear-felling plots referred to below (pp. 10, 11, 19).

<sup>3</sup> The numbers in brackets are the reference numbers of the soil samples.

<sup>4</sup> The methods adopted are described in Appendix I (at end of Part II).

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(2) Plants dependent on others for mechanical support ("Guilds" of Schimper).

(a) Climbers and similar forms.

(b) Epiphytes.

B. Heterotrophic (saprophytes and parasites).

This scheme is slightly modified from that used in describing the structure of the British Guiana rain forest. The wealth of forms of which the Mixed forest is built up is so great that any classification will give an over-simplified picture. Besides plants which are intermediate between some of the above classes, there are others which for part of their lives belong to one class and for another part to another, e.g. the "strangling" figs, *Ficus* spp.

(a) *Stratification of trees.*

The method mainly relied on for studying the stratification of the Mixed forest was felling and measuring two sample strips and constructing profile diagrams (Figs. 2 and 3, folders) from the data so obtained. Since descriptions of the structure of tropical forests derived merely from general observation are necessarily vague and often misleading, these two profile diagrams will mostly be left to speak for themselves, and only a few comments need be made on them.

The two sample strips were each  $200 \times 25$  ft. ( $61 \times 7.6$  m.). One ran along the summit of a small ridge, the other along the contour on the side of the same ridge. In neither strip was the ground quite level, though it has been drawn so on the diagrams: but as the difference of level between one part of a strip and another was probably never more than 10 ft. (3 m.), only a slight error has thus been introduced. On each strip all trees over 25 ft. (7.6 m.) high were measured (total height, height of lowest branch, height of lowest foliage, width of crown, diameter of trunk at breast height or above the buttresses). For each tree the vernacular name, the presence of flowers or fruit, buttresses and epiphytes were noted. Large lianes were also recorded.

In both diagrams the following strata can be recognised:

(i) A layer of trees averaging about 110 ft. (34 m.) high. The crowns are about 20 ft. (6 m.) deep and have a spread usually greater than their depth. The crowns of neighbouring trees of this layer are not as a rule in contact laterally, hence the very uneven surface of the forest when seen from above (Pl. I, phot. 2). A marked gap separates the bases of the crowns of the trees in this layer from the tops of trees in the next layer. A large proportion of the trees forming this layer belong to the Dipterocarpaceae and only a few other families are represented in it.

(ii) A layer of trees averaging about 60 ft. (18 m.) high. The crowns average about 15–20 ft. (4.5–6 m.) deep, but have a spread usually less than their depth. They are usually in contact with their neighbours on all sides. To this layer, if to any, the misleading expression "canopy" should presumably

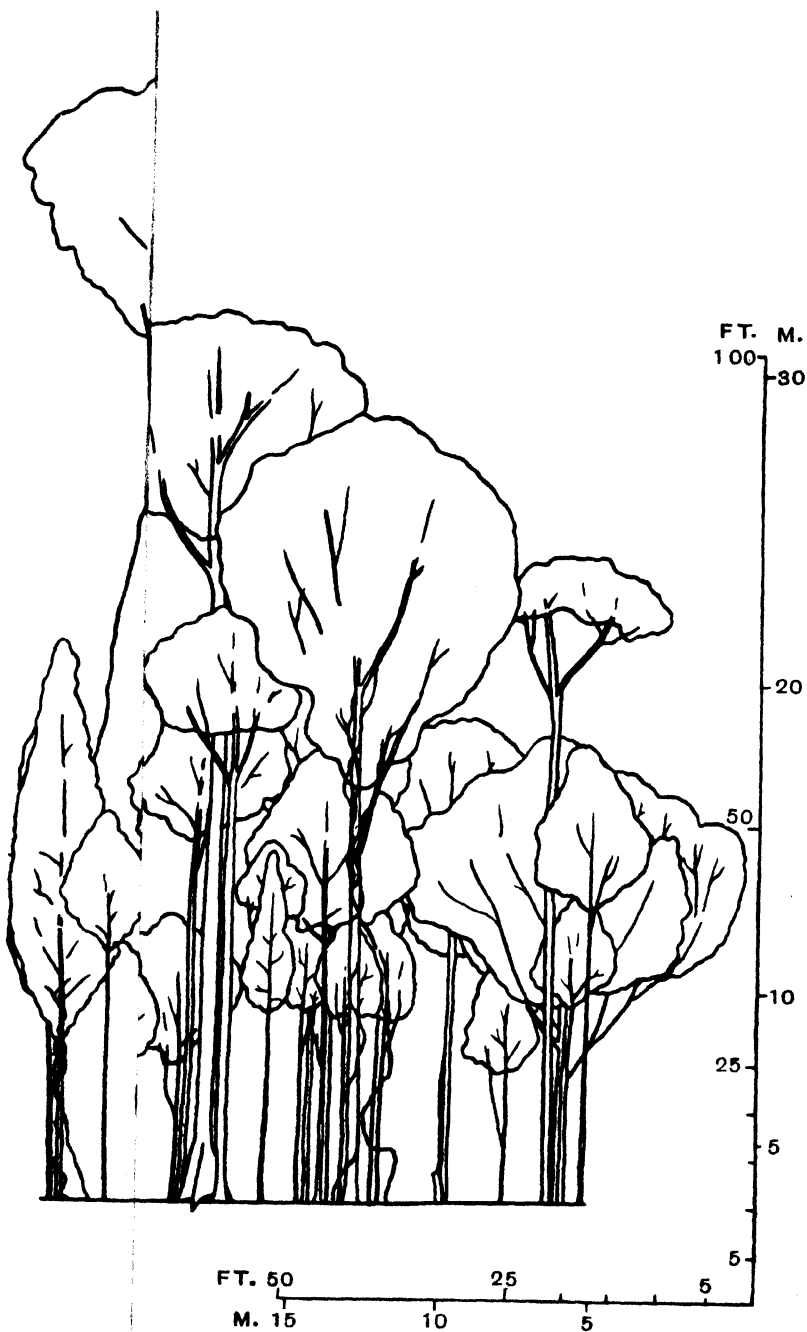


FIG. 2. Profile.) wide. The following are based on measurements and drawn strictly to scale: tessary as a convention to draw the crowns as compact and dense though that is of



be applied. This layer consists of very numerous species belonging to a great variety of families: as well as dicotyledonous trees there are a few tall palms (none on the clear-felling plots), but these are rare.

(iii) A layer of small trees ("undergrowth trees") about 25 ft. (8 m.) high on the average. These are characterised by their very deep narrow crowns of conical shape, which are seldom more than 10 ft. (3 m.) in spread, but commonly exceed 15 ft. (4.5 m.) in depth. A large proportion of them are young individuals of species belonging to layers (i) and (ii). As in the British Guiana forests, the Annonaceae occupy an important place among the true undergrowth species.

There is no discontinuity separating (ii) and (iii); the intervening region is filled with trees of every intermediate height. Observation over the whole district, however, shows that there is a definite group of species which average about 60 ft. high when mature and do not flower when much smaller, and another group which is about 25 ft. high when mature; the latter begin to flower when very small. The absence of discontinuity between strata (ii) and (iii) is therefore due to the abundance of immature trees belonging to stratum (ii) when mature and to the presence of members of stratum (iii) taller than the average. Probably over half the trees in the undergrowth stratum (iii) are immature individuals of species belonging to strata (i) and (ii). Such immature trees have generally rather shallower and relatively broader crowns than the true undergrowth species.

Two features of the arrangement of the trees are worth noting. There is a marked tendency for the undergrowth and slightly larger trees to be more abundant close to the trees of layer (i) than between them. The reason for this may be that when the crowns of the large trees raise themselves above the canopy a gap is made through which an abnormally large amount of light penetrates, and this encourages the growth of seedling and sapling trees on the forest floor below.

The other striking feature is the extraordinary difference in the density of the trees on the crest and side of the ridge: the plot on the crest contained ninety-one trees over 25 ft. and thirty-one over 50 ft. high, that on the side only forty-four trees over 25 ft. and thirteen over 50 ft. high.<sup>1</sup> This difference is presumably due entirely to the greater amount of light received by the summit. In spite of the much greater number of trees per unit area, the ridge-top forest seemed less shady than that on the ridge sides.<sup>2</sup> It is only on very narrow ("knife-edge") ridges that this difference in density is well marked.

The picture of the forest structure just given applies, as far as could be made out, to all the Mixed forest in the Mt Dulit district. The height of the

<sup>1</sup> Or fifteen trees over 8 in. (20 cm.) diameter on the summit and nine on the side. Cf. the similar increase in the density of the forest on the banks of large rivers in British Guiana.

<sup>2</sup> As all the expedition's stopwatches succumbed quickly to the damp, no actinometric measurements could be made.

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tallest stratum of trees varies considerably from place to place, and the gap separating strata (i) and (ii) is probably in many places less definite than on the plots. The two profiles probably represent forest rather less tall than the average: at any rate individual trees of stratum (i) are frequently much taller than any shown in the profiles. The tallest tree measured grew in rocky Mixed forest near a torrent: it was 150 ft. (45.7 m.) high and belonged to the Annonaceae (R. 1187). Exceptionally tall trees, however, usually belonged to the Dipterocarpaceae, e.g. *Shorea* spp., etc., or Leguminosae, e.g. Tapang (*Koompassia* sp.?). Some of them may have been as much as 200 ft. (61 m.) high.<sup>1</sup>

Throughout the Mixed forest there was a tendency for the bigger trees to grow together in groups of two or three. This feature, however, is not shown on the profiles.

When the heights of the trees on the profile strips are grouped together into height classes and the number of trees in each is plotted, a curve is obtained similar to that given for the British Guiana forest except that the smaller upper maximum is much higher (105–114 ft., instead of 76–85 ft.).

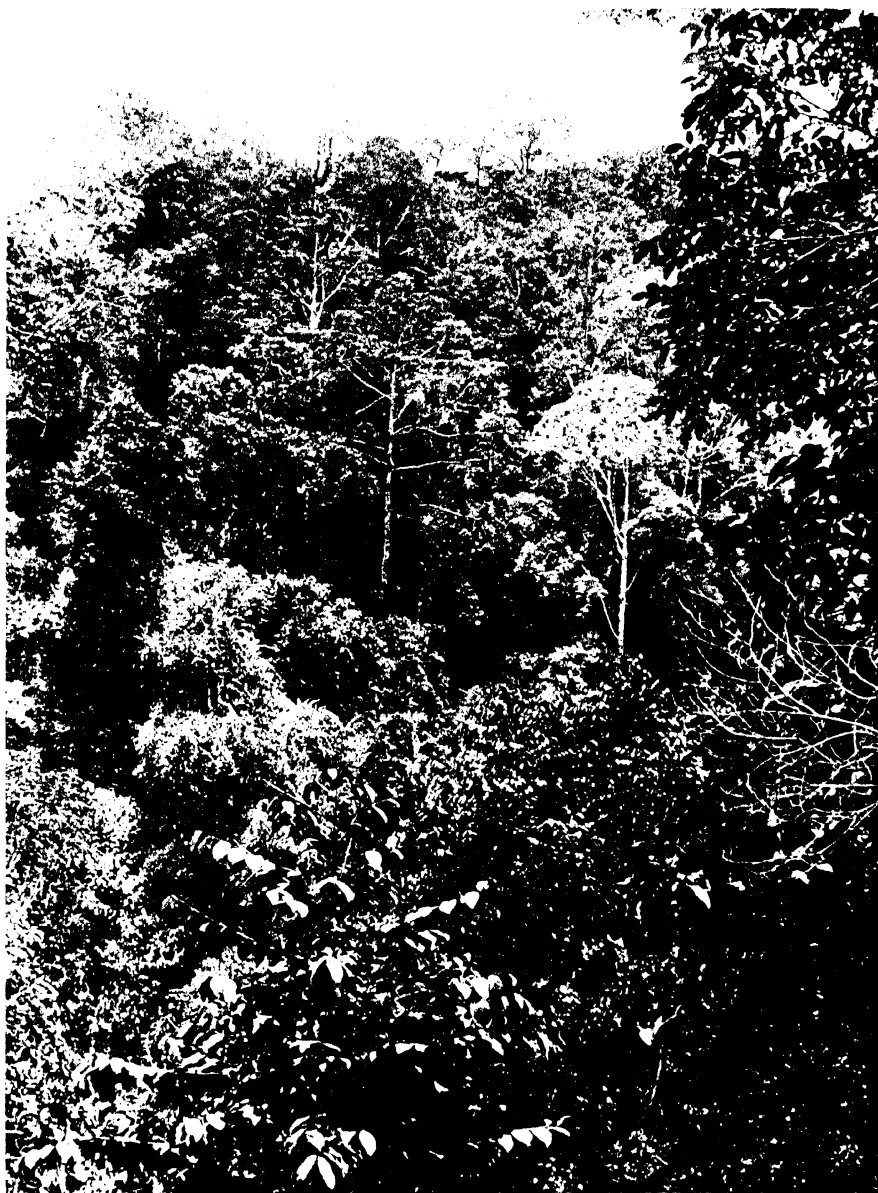
The numbers of trees in flower or young fruit at the time of felling (October and November) were distributed among the height classes in much the same way as in the British Guiana forest. As there, the percentage of trees in flower is very small in the lower level, presumably partly because the flowering season of the smaller trees extends through the whole year (cf. p. 8) and partly because the lower levels include a high proportion of immature trees: at about 35 ft. (10 m.) it suddenly increases. Very few first-storey trees were in flower during the period of the work (cf. p. 8).

The stratification of the trees on the two sample strips is closely comparable with that described for evergreen Dipterocarp forests in some other parts of the Malayan region, e.g. Mt Maquilang in the Philippines (Brown, 1919, pp. 30 *et seq.*). In the lowland "High Forest" of the Malay Peninsula, to judge from Foxworthy's description (1927, pp. 7–8), the chief differences are that all the storeys are considerably higher (the first storey averages "something more than 150 ft."), and that an extra storey is intercalated between what correspond to the second and third storeys on the sample strips.

If the Dulit Mixed forest is compared with the Mixed forest of Guiana (cf. Davis and Richards, 1933, Fig. 6 and pp. 362–71), the stratification of the trees is found to be to a large extent similar in both, though there are some differences.

In the Guiana forest "the trees form only two distinct strata, an irregular canopy of about 24 m. average height and undergrowth trees up to about 14 m. high. Above the former many trees of up to 42 m. stand out incompletely, while here and there are exceptionally tall trees which have their

<sup>1</sup> Beccari measured an individual of *Abauria* (*Koompassia*) *excelsa* Becc. 230 ft. (70.1 m.) high on the Entabei River (Ulu Rejang) in Sarawak (Beccari, 1904, p. 330).



Phot. 3. Mixed forest with many large Dipterocarps. Mt. Dulit (alt. *c.* 400 m.).

RICHARDS—RAIN FOREST OF MOUNT DULIT, SARAWAK

*Face p. 12*





whole crown clear of their neighbours" (Davis and Richards, 1933, pp. 383-4). Stratum (iii) on the Dulit strips corresponds exactly with the layer of undergrowth trees in Guiana: it is of approximately the same height, and the constituent trees have a very similar general appearance and mode of branching. The irregular top storey of the Guiana forest is, however, represented on the Dulit sample strips by two distinct strata separated by a gap. The lower of these is of about the same average height as the lower part of the canopy on the Guiana sample strip and the upper is taller than the upper part of the canopy, but its average height is not as great as that of the "outstanding trees" in the Guiana forest. If, however, the profile diagrams for the two Dulit strips and the Guiana strip respectively are compared, this difference in the upper layers does not seem as clear-cut as it does when put into words. There is no evidence of any fundamental difference in stratification between the Dulit and the Guiana Mixed forest.

(b) *Buttressing.*

Throughout the Mixed forest a large proportion of the bigger trees have plank buttresses. The majority of these buttressed trees belong to the first storey, in which there are hardly any unbuttressed trees. The taller trees of the second storey are also often buttressed, but the buttresses are usually smaller and less wide-spreading. None of the undergrowth trees is buttressed, but species belonging to the first and second storeys often begin to develop buttresses when still in the lower levels of the forest. *Within this type of forest* there seems to be a rough relation between the mature height of the tree and the size of the buttresses, though many other factors are involved. Thus the most strongly buttressed species in the Mixed forest was the Tapang (*Koompassia* sp.?, Leguminosae), which was also one of the tallest.

On the whole the "amount of buttressing" (i.e. the relative frequency of buttressed trees and the size of their buttresses) did not vary much in different habitats within the Mixed forest. It did, however, tend to be somewhat greater on the ridge crests and on the steep rocky sides of stream valleys, i.e. where the soil was particularly shallow.

Trees with "flying" buttresses and with round stilt roots are rare in the Mixed forest.

(c) *Shrubs and herbs.*

The undergrowth of virgin Mixed forest is generally not very thick and, as has been mentioned, it is usually possible to walk about in it without cutting paths. The density of the undergrowth varies, however, with the density of the canopy. On the ridge tops, where there are many first- and second-storey trees per unit area, there is very little undergrowth, and it is possible to see for a considerable distance ahead: the ridge sides and valleys, on the other hand, have fewer large trees per unit area and denser undergrowth.

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There is no very definite stratification of the vegetation below the level of the undergrowth trees, but it is convenient to divide it into (a) the shrub layer, averaging 4 m. high, and (b) the ground flora, averaging about 1–2 m.

The shrub layer is composed of young trees, palms and a great variety of dicotyledonous shrubs. The first component probably always exceeds the other two in number of individuals. The palms are represented by many genera and species (*Licuala* spp., especially common and characteristic), but are seldom very abundant.<sup>1</sup>

The ground flora is patchy. On large areas, especially on the ridges, it may be represented only by isolated plants at long intervals; elsewhere it may be fairly dense, though seldom as dense as in an average European deciduous forest.

The ground flora consists of tree seedlings, ferns and herbs; one or two rare species of very small palms may also be looked on as belonging to it. The tree seedlings everywhere outnumber the other components. Some counts made on metre quadrats on a typical ridge gave the following results:

	No. of shoots under 1 m. high	
	Crest of ridge Sum of 6 quadrats	Side of ridge Sum of 6 quadrats
Herbs	78	17
Ferns and <i>Selaginella</i> sp.	14	26
Young trees and other woody plants	94	90
	186	133

The greater abundance of ferns on the side of the ridge is characteristic and is probably related to the damper and more shady conditions at the ground-level.

The herbaceous component of the ground flora is very rich floristically in the Mt Dulit Mixed forest, as everywhere in Borneo, which differs very markedly in this respect from British Guiana. There is considerable variation in the floristic composition of the ground flora from place to place, often without any obvious relation to changes in soil or other conditions. Thus many species tended to be common on one or two neighbouring ridges, but were found nowhere else in the district. Comparatively few families are represented in the ground flora, but several of them include a very large number of species. The chief are Begoniaceae, Melastomaceae, Gesneriaceae, Zingiberaceae, Araceae and Cyperaceae. The Zingiberaceae are much the richest family in species, but scarcely ever become social and cover large areas as they often do in the secondary forests.

The ground flora has far more variety of form and colour of foliage than any other stratum of the forest. Many curious leaf features—such as variegation (various Melastomaceae, Acanthaceae, Gesneriaceae and Araceae), red markings (some orchids), velvet (*Neckia* sp. R. 1413, Araceae, some orchids)

<sup>1</sup> Undergrowth consisting largely of a small species of palm was met with on the ridge of Gunong Laiun at c. 800–1000 m., but this was hardly normal Mixed forest.

and metallic surfaces (*Mapania monostachya* Uitt., R. 1801, with brilliant metallic blue-green leaves)—are found only among the herbs of this layer. Drip-tips are rare: they are far more characteristic of the young and undergrowth trees. A curious feature which is widespread among the ground flora is the production of the flowers just above the surface of the soil, e.g. on short branches of the main axis (some Zingiberaceae), on rhizomes running along the surface of the soil (*Forrestia* sp., R. 1078), on long flexible scapes lying loosely on the surface of the ground (*Cyrtandra penduliflora* Kraenzl., R. 1275), etc. A similar habit is found even in one of the undergrowth trees (R. 1407, Annonaceae), which bears its flowers on tufted gnarled twigs about 10 cm. long, borne just where the trunk emerges from the ground.

There are no ground mosses in the Mixed forest at low altitudes, except rarely on very steep slopes.

(d) *Climbers and similar forms.*

The climbing plants of the Mixed forest may be divided for convenience into:

(i) *Climbers on first- and second-storey trees.* Among these are the rotans (several genera of climbing palms) and an enormous number of species of dicotyledonous lianes with thick woody stems. The latter are not very abundant in undisturbed forest, but are never entirely lacking. They are particularly scarce on ridge tops. Rotans are fairly abundant everywhere, but especially so in undisturbed forest far from villages, as large specimens are much sought after by the natives. The crowns of the rotans are a characteristic feature of the canopy of the forest when seen from above.

This group includes twiners, hook-climbers, a few root-climbers, and other types not easy to classify. Twiners probably predominate.

(ii) *Climbers on undergrowth trees.* This group cannot be sharply divided from the last. It includes comparatively few species, but they are very varied. As well as flowering plants a few ferns, e.g. *Trichomanes* sp., and two common species of *Gnetum* (*G. Gnemon* L., R. 1076 and 1077, and another sp., R. 1450, etc.), belong here. Root-climbers form a large percentage of this group, but sometimes climbing by aerial roots is combined with other methods, e.g. *Hoya* spp., which both twine and have aerial roots.

With the true climbers may be included the so-called "strangling" figs, species of *Ficus*, which, like the South American *Clusias*, begin life as epiphytes and send down roots to the ground. Unlike the *Clusias*, they ultimately become large independent trees (first storey) and they usually kill their "hosts". They were not very abundant in the Mt Dulit region, though there seemed to be a number of different species.

(e) *Epiphytes.*

One of the most striking features of the Sarawak rain forest, especially when compared with that of tropical South America, is the poverty of the

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epiphytic vegetation both in species and individuals. Thus, while on the two clear-felling plots in British Guiana 24 per cent. of the trees over 25 ft. (7.6 m.) high bore vascular epiphytes and one tree might have often four or even five or six species, in the clear-felling plots at Mt Dulit only 13 per cent. of the trees on the top of the ridge and 11 per cent. of those on the slope had any epiphytes other than mosses and lichens: no tree on either strip had more than four species and most had only one. Even in gulleys and by torrents epiphytes are not much more abundant. This poverty of the epiphytic vegetation is probably characteristic not only of Sarawak, but of the lowland forests of the Malayan region generally. As the climatic conditions in Malaya would seem to be even more favourable to the growth of epiphytes than that of most of tropical America, the cause is perhaps historical. The Malayan flora seems never to have produced a family able to play the role of the Bromeliaceae, which in South America are much the most abundant family of epiphytes and often act as pioneers.

Two communities of epiphytes are found in the Mixed forest:

(i) *Society of shade epiphytes*. This is found in the undergrowth and reaches its upper limit at about 12 m. above the ground, though individual members may reappear on the branches of large trees with dense crowns, e.g. some filmy ferns were not uncommon in the undergrowth and in the crowns of large trees, though absent at intermediate levels. Except for occasional seedling orchids, which apparently never develop, this society consists entirely of ferns, Selaginellas (rare) and bryophytes. The shade society is best developed near torrents: on ridges it becomes very scanty.

(ii) *Society of sun epiphytes*. This lives in only slight shade on the trunks and crowns of trees above 12 m. from the ground, but some of the constituent species may be found at lower levels if the illumination is good. Thus the fern *Humata repens* (L. fil.) Diels (R. 1466, etc.), which normally occurred only on the branches of the tallest trees, was once found at less than 1 m. from the ground on the crest of a "knife-edge" ridge. This society consists of both herbs and shrubs. About nine families are represented: Orchidaceae and Gesneriaceae (*Aeschynanthus* spp.) are the most numerous. The semi-parasitic Loranthaceae, which are very abundant and widespread in the crowns of the taller trees, may also be included here.

Some members of this society, e.g. the ferns *Asplenium nidus* L. and *Drynaria quercifolia* (L.) J. Sm., seem to prefer the trunks of the trees to the branches. Some epiphytes, e.g. certain orchids, are confined to very large (and presumably very old) trees. A large proportion of the sun epiphytes have more or less succulent leaves.

Nearly all of them are fairly constantly associated with ants and many have specialised internal cavities in which the ants live, e.g. *Myrmecodia* sp. and *Lecanopteris crustacea* Copel. (R. 2259). The importance of the

ants to the plants is more likely to be as collectors of humus than as protectors against other insects. It seems significant that so many of the myrmecophytes of the Mixed forest were epiphytes.

(f) *Parasites and saprophytes.*

Besides the green epiphytic Loranthaceae the only parasitic flowering plant met with in the Mt Dulit district was *Mycetanthe* cf. *Lowii* (Becc.) Hochr., (R. 1106). This was found only once, on the roots of a liane in rocky Mixed forest at c. 300 m.

Like most other rain forests, the Mt Dulit Mixed forest has a society of small colourless saprophytes. Its distribution is very patchy. Over large areas it is entirely absent or represented by rare and isolated individuals of the commonest constituent species only: here and there are patches, often only a few square metres in area, in which a number of individuals of three or four species occur together. This type of distribution of these small saprophytes has been noticed several times and in several parts of the Tropics (Malaya, Schlechter, quoted in Winkler (1914), p. 201; south-east Borneo, Africa, Winkler (1914), p. 201; British Guiana, Davis and Richards, Part I, p. 372 and Part II, p. 116). These patches of saprophytes occur usually in the deepest shade on rather moist level ground where the dead leaf carpet is thicker than usual.

In the Mixed forest the members of this society are: *Epirixanthes elongata* Bl. (R. 1289, etc.), (Polygalaceae), common; *Sciaphila* sp. (R. 1320, 1611, 1152) (Triuridaceae), rather common; *Gymnosiphon aphyllum* Bl. (R. 1267 and 1344), *Thismia* sp. (R. 1268), *Burmanniea* sp. (R. 1379) (Burmanniaceae). There are also several species of colourless saprophytic orchids, but these do not usually occur associated with the species just mentioned.

(g) *Internal climate.*

Observations of temperature and humidity were made in Mixed forest on the slope of a low ridge on the right bank of the Tinjar for a complete week. The instruments were placed on a shelf about 2 dm. above the surface of the ground in a small palm-thatched shelter, which allowed free circulation of air, but protected them from rain and sun-flecks. Wet- and dry-bulb thermometer readings were also taken at heights of 1, 9, 17 and 27 m. on a neighbouring first storey tree, which was climbed by means of a rope ladder.

The following table shows the results of the temperature readings in the shelter:

Date	Maximum °C.	Minimum °C.	Range °C.
Oct. 24th	28.5 (—)	23.5 (—)	5.0 (—)
25th	29.25 (—)	24.25 (—)	5.0 (—)
26th	26.75 (29)	23.0 (23)	3.75 (6)
27th	28.0 (29)	23.0 (22)	5.0 (7)
28th	27.0 (27)	22.25 (22)	5.25 (5)
29th	26.0 (27)	22.75 (23)	3.25 (4)
30th	27.25 (27)	23.25 (23)	4.0 (4)
Mean	27.5 (28)	23.1 (23)	4.5 (5)

The figures in brackets are the readings made on the same day in the Base Camp (open clearing). Readings in forest to near 0.25°: readings in Base Camp to nearest degree.

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Thus there appears to be no significant difference in temperature conditions between the forest undergrowth on the side of a ridge and a shaded place in a small open clearing.

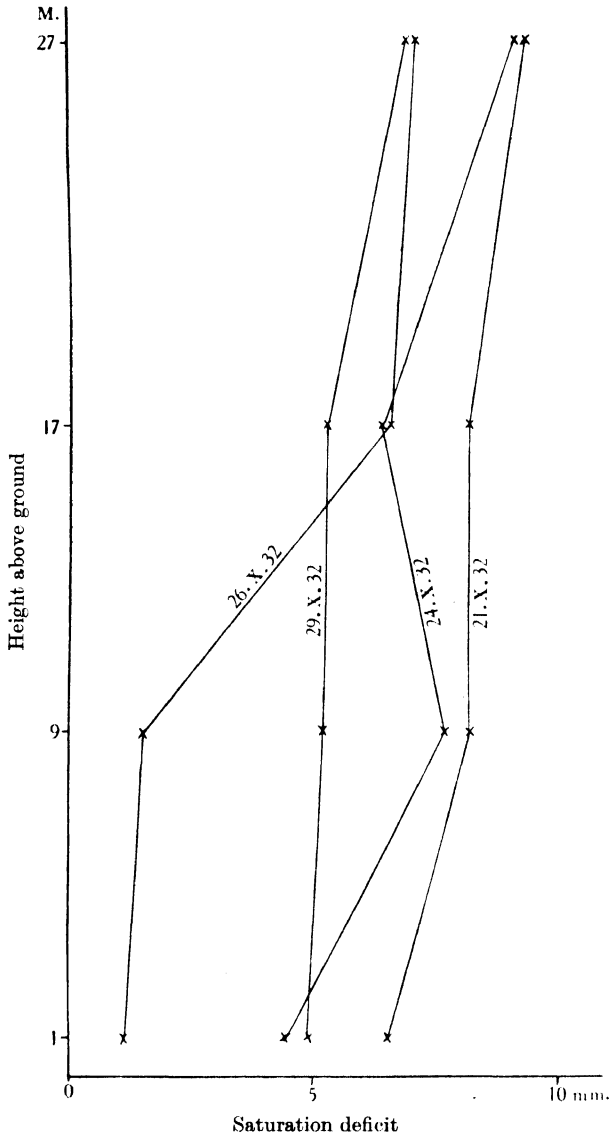


FIG. 4. Vertical gradient of saturation deficit on tree in Mixed forest, Kapah river, Mt Dulit. Calculated from wet- and dry-bulb whirling psychrometer readings. All readings were made at noon and the weather conditions were as follows: October 21st, sunny with light clouds: October 24th, sun with few clouds, previous night dry: October 26th, sun with clouds, rain on previous night: October 29th, clouds and weak sun, a little rain on previous night.

The humidity curves in the forest show some slight differences from those obtained at the Base Camp.<sup>1</sup> There is the same almost absolutely constant period at night when the humidity remains at saturation or a few per cent. below. A similar level high phase was found by McLean (1919) in the rain forest at Rio de Janeiro. This high level was reached at times varying between  $1\frac{1}{2}$  hours before and  $2\frac{1}{2}$  hours after sunset. In the morning the humidity did not begin to fall till 9 a.m. or even later, while in the Base Camp it began to fall almost immediately after sunrise (about 6 a.m.). The minimum was reached rather earlier (about 12) than at the Base Camp: its mean value was 72 per cent. (61 per cent. for October 13th–22nd at Base Camp) and the absolute minimum was 64 per cent.

*The vertical gradient of saturation deficit* at different levels in the forest is shown diagrammatically in Fig. 4. The curves do not indicate an abrupt change of conditions at any level, as might rather have been expected from the relatively greater density of the undergrowth compared with the higher levels.

No measurements of *light* were made in the Mixed forest. Since most descriptions of rain forests give an exaggerated idea of the shade, it is perhaps worth emphasising that sun-flecks are found everywhere in the Mixed forest. As Giesenhagen points out (1910, pp. 727–8), the gloom of the tropical rain forest is not comparable with that in a northern coniferous forest: what he says of the rain forest of Java and Sumatra—"Am ersten lässt sich das Licht im Urwalde noch vergleichen mit dem eines alten, lichten hochstämmigen Buchenwaldes im Frühlingsgrün"—applies very well to the Mixed forest of Mt Dulit.

### (iii) *Floristic composition*

The floristic composition of the first and second strata of the trees in the Mixed forest was investigated by enumerating all trees over 8 in. (20 cm.) diameter<sup>2</sup> on a sample plot according to their vernacular names.

The plot was 400 ft. (122 m.) square (1.418 hectares). The method of marking it out and listing the trees was similar to that used in British Guiana (described in Davis and Richards, Part II (1934), p. 107). The trees were grouped into three diameter classes, 8–16 in. (20–41 cm.), 16–24 in. (41–61 cm.) and over 24 in. From the two clear-felling strips (see p. 10) a curve (Fig. 5) was drawn of diameters plotted against heights: this indicated that trees of 8 in. diameter average about 60 ft. (20 m.) high and those of 16 in. about 90 ft. (28 m.) high. The 8–16-in. diameter class therefore corresponds to a part of the second storey and the other two diameter classes to the first storey.

<sup>1</sup> The Mixed forest records were obtained on October 24th–30th inclusive. The Base Camp records with which they were compared were for October 13th–22nd inclusive.

<sup>2</sup> Diameters here, as elsewhere in this paper, refer to breast height or above the buttresses. They were not measured with callipers, but estimated with the help of a tape measure.



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The vernacular names<sup>1</sup> were determined by a Malay forest guard from Marudi. As with the British Guiana vernacular names, they were of various values, some probably corresponding to a single species, others to a group of similar species, and others again to a large number of different species with certain characters in common. In making determinations the forest guard relied largely on the characters of the bark and blaze, but also took into account the size and form of the leaves.

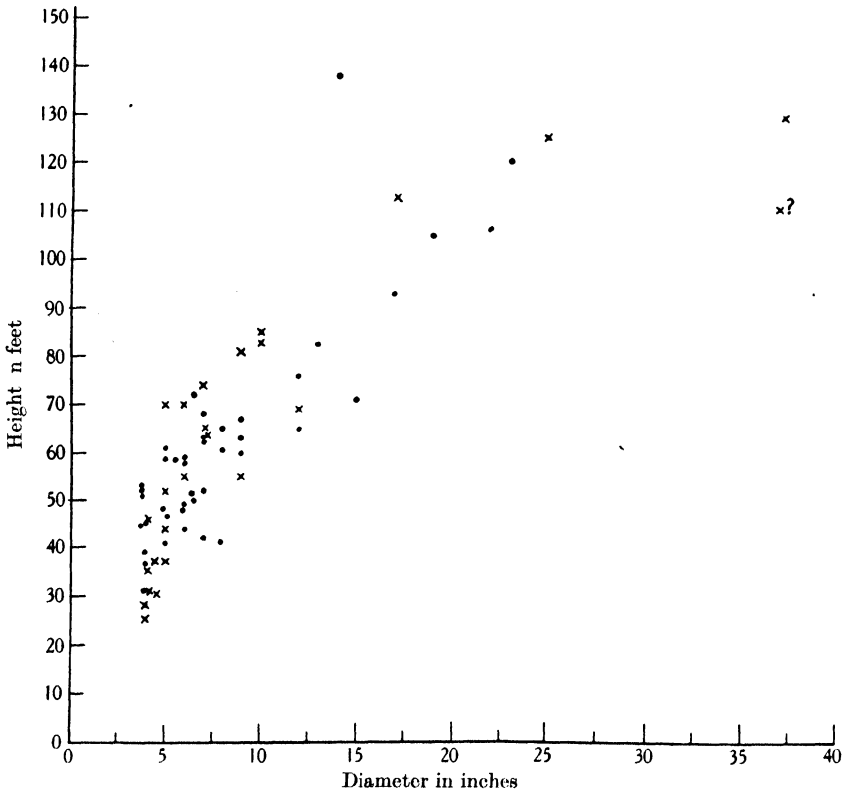


FIG. 5. Height/diameter diagram for clear-felled strips. Mixed forest, Kapah river, Mount Dulit. Dots = trees on strip on summit. Crosses = trees on strip on side of ridge.

This man had not previously carried out enumerations of this kind, and owing to the Malay notion of politeness, which consists of always giving a positive answer to a question, even if it is known to be wrong, some of the names may have been fictitious. The results can therefore be taken as giving only a rough idea of the floristic composition. Owing to the very large number of species involved, even in this one plot, it was impossible to identify more

<sup>1</sup> Most of these names were Malay (Sarawak or Brunei dialects), but some may have been of Iban or other native origin. Some of them were the same, or nearly so, as names used in the Malay States, Sumatra, etc.: in Sarawak they are probably used for similar, but not identical, trees.

than a fraction of the names even approximately. In spite of these difficulties the enumeration revealed several interesting facts.

Owing to the absence of primary forest on even moderately level ground the plot had to be on a fairly steep slope on the side of a typical knife-edge ridge. The upper border of the plot ran along the crest of the ridge, the altitude of which must have been between 100 and 200 m. above sea-level.

The results may be summarised<sup>1</sup> as follows:

Diameter class	Number of trees			Totals
	8-16 in. (20-41 cm.)	16-24 in. (41-61 cm.)	Over 24 in. (61 cm.)	
On plot	199	21	41	261
		62		
Per hectare	140	15	29	184
		44		

Number of "species" (by vernacular names) on plot	
Trees over 8 in. (20 cm.) diameter	Trees over 16 in. (41 cm.) diameter
98	32

These estimates of the number of species are rough lower limits, as more than one vernacular name was probably rarely given to one species, but some of the vernacular names may have included more than one species.

The most abundant "species" was *Medang Lit* (not a Dipterocarp) of which there were twelve individuals (4.5 per cent. of all trees over 8 in. diameter), but all in the 8-16-in. diameter class and therefore belonging to the second storey. *Meranti daging* (Dipterocarpaceae,<sup>2</sup> probably *Shorea* sp.), *Njalin batu* and *Ubah kelat* (perhaps *Eugenia* sp.) were each represented by nine individuals (3.4 per cent.). *Meranti daging* and *Marakah batu*, both of which were probably Dipterocarps, were the most abundant species over 16 in. diameter and were each represented by six individuals (9.7 per cent. of all trees over 16 in. diameter).

It is clear therefore that the Mixed Dipterocarp forest is rain forest of the "classical" type, in which no one species attains anything approaching dominance. The family dominance of the Dipterocarpaceae is, however, strongly marked. Trees probably belonging to this family form 17 per cent. of trees over 8 in. diameter and 44 per cent. of those over 16 in., but both these figures are almost certainly underestimates.<sup>3</sup> The remainder of the trees on the plot belong to a very large number of families.

<sup>1</sup> The full results are given in Appendix II (at end of Part II).

<sup>2</sup> The characteristic venation of fallen leaves was relied on to some extent in identifying members of this family, in addition to evidence given by the Malay enumerator.

<sup>3</sup> Winkler (1914, p. 198) remarks that the Dipterocarpaceae seem to be rare in the lowlands of south-east Borneo, as he failed to find the characteristic winged fruits. This, however, by itself is not good evidence of their rarity, as at Mt Dulit Dipterocarp fruits were very rare though a fruiting season had occurred only a short time previously. The fruits must either decay rapidly or, more probably, get eaten up by animals.

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The above data may be compared with the following taken from Brown's description (1919, pp. 53-5) of a sample plot 0.25 hectares in area in the Dipterocarp forest of Mt Maquilung, Philippine Islands:

Diameter class	<i>Number of trees</i>	
	40 cm. and over	20 cm. and over
	On plot	16
	Per hectare	64

The most abundant tree species formed 19.6 per cent. of the trees over 20 cm. and 18.7 per cent. of those over 40 cm. diameter: as on the Dulit plot, it was not a Dipterocarp and belonged to the second storey. Dipterocarpaceae formed 12.5 per cent. of both the 20 cm. and over and the 40 cm. and over diameter classes. On other sample plots in Philippine Dipterocarp forests for which figures are given by Whitford (1909) the most abundant species always forms a larger percentage of the total stand than on the Dulit plot. The percentage of Dipterocarps among trees of 40 cm. diameter and over varies from 33.1 to 89.4.

As compared with the Mixed forest of Moraballi Creek, British Guiana (Davis and Richards (Part II), 1934, pp. 117-19), the most striking features in the floristic composition of the Dulit Mixed plot is that the mixture of species is even greater and the absence of dominance even more marked. The number of species 8 in. and over in diameter on the Guiana plot was only about fifty-seven as compared with ninety-eight on the Dulit plot. While the most abundant species in the 8 in. and over diameter class on the Guiana Mixed plot formed 12.7 per cent. and that in the 16 in. and over class 15.6 per cent. of the total number of individuals, at Dulit, as we have seen, the corresponding figures are only 4.5 and 9.7 respectively. The preponderance of a single family, which is such a noticeable feature of the Mixed forest of Dulit, was, however, much less marked in that of Guiana.

The floristic composition of the shrub and herb layers in the Mixed forest was not studied systematically, but it was evidently somewhat different on ridge crests and ridge sides. On the crests species intolerant of deep shade were often present, e.g. *Gleichenia linearis* (Burm.) Clarke, *Eurycoma longifolia* Jack. ? (R. 1012) and *Anisophyllea disticha* Baill. (S. 32). The last species was frequent in "Heath forest", but on heavy soils was only found on top of knife-edge ridges and in second growth. The *Eurycoma* was also a common "Heath forest" species.

### (iv) *Mid-mountain forest*

On the Tinjar side of Dulit, from about 450 m. to the lower boundary of the Moss forest, and in the corresponding zone on Laiun, the Mixed forest differed from that at lower altitudes. Owing to lack of time, it was not possible to make an intensive study of this type of forest and to determine whether it was merely a modification of the Mixed Dipterocarp forest or whether it would be better regarded as an independent type. It is certainly much more like the





Phot. 4. Road through "Heath forest", Forest Reserve, Marudi.



Phot. 5. "Heath forest", Koyan valley (alt. *c.* 750 m.) showing dense undergrowth.



Phot. 6. Moss forest, closed facies, Mt. Dulit. (alt. *c.* 1230 m.). Note straggling bamboo (R. 2013).



Phot. 7. Moss forest, Mt. Dulit.

RICHARDS--RAIN FOREST OF MOUNT DULIT, SARAWAK

Mixed than either the "Heath" or the Moss forest types. In many respects it seems to resemble closely the "Mid-mountain forest" found on Mt Maquiling in the Philippines from 600 to 900 m. (Brown, 1919, pp. 76-97).

How far this forest differed in structure from that at lower altitudes was not easy to determine owing to the steepness and irregularity of the ground, but probably at least some of it, like the Mid-mountain forest of Mt Maquiling, had only two layers of trees, the first storey of the clear-felling strips being absent. The herb layer is thicker and richer in species than in the lowland forest. Epiphytes, both vascular and non-vascular, are far more abundant; several species are frequent which are absent at lower altitudes, e.g. *Rhododendron lineare* Merrill (R. 1441). Though mosses and liverworts are not nearly as luxuriant as in the Moss forest, they are much more abundant than in the lowland forest. Another characteristic of the mid-mountain forest is that mosses, e.g. *Leucobryum aduncum* Doz. and Molk. (R. 2093), *L. javense* (Brid.) Mitt. (R. 1504), are not uncommon on the ground.

### (3) "HEATH FOREST"

On sandy soil in the upper Koyan valley (on the south-western side of Mt Dulit) a type of primary rain forest was met with which differed very strikingly from the Mixed forest both in aspect and in floristic composition. Its most obvious characteristics were the dense undergrowth, the comparatively small amount of buttressing of the larger trees and, above all, its lightness. The impression it gave was rather of an Australian forest than of the normal gloomy tropical rain forest. In some respects also, as will be seen later, it recalls European heath vegetation.

Forest of a similar type was also seen on white sand soils (derived from Middle Miocene sandstone) at Marudi (Claudetown or Baram) on the Baram, about 80 km. from Mt Dulit.

This peculiar forest was evidently similar to that which has been described by H. Winkler from south-east Borneo (Dutch territory) and called by him "Subxerophilous Primary forest" or "Heath forest" ("Heidewald") (1914, p. 202). The latter term is convenient and, as Winkler observes, expresses the fact that the forest in question is an edaphic, not a climatic, type.<sup>1</sup> The resemblance between Winkler's "Heath forests" and those of Sarawak extends even to small details; Winkler's photograph of a forest road near Djihi, Dutch Borneo (1914, Pl. 4), might easily have been taken on the road through the Marudi Forest Reserve (Pl. III, phot. 4).

As the Koyan forest was very inaccessible, it could not be studied at all thoroughly: the following account is therefore based partly on the Marudi forest as well. Though there were a number of differences, these two areas of

<sup>1</sup> At the same time the name perhaps suggests a more far-reaching analogy with Heath than there actually is. However, until the vegetation of the whole of Borneo is better known, it is hardly possible to give any of the types of vegetation more than provisional names.

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forest were on the whole very similar, in fact surprisingly so, considering the difference in altitude (nearly 750 m.). Further research will perhaps show that the "Heath forest" of the type represented by the Koyan sample plot is a montane variant of the lowland "Heath forest" and related to it much as the "Mid-mountain forest" (cf. p. 22) is related to the lowland Mixed forest.

The climate of the Koyan "Heath forest" is no doubt somewhat cooler and damper than that of the Dulit Mixed forest, but that of Marudi, situated far from mountains, is probably drier and possibly slightly hotter, so that the resemblances between the two areas of "Heath forest" clearly must be due to edaphic causes.

### (i) *Habitat and soil conditions*

In the Koyan valley the "Heath forest" extended from an altitude of about 750 m. upwards towards the crest of the Dulit ridge. It no doubt also extended farther down the valley, but could not be followed farther owing to the uninhabited and difficult nature of the country. Above an estimated altitude of 1100 m. it was replaced by Montane rain forest ("Moss forest"). Though the boundary, like that between the Mixed (Mid-mountain) forest and the Moss forest, was sharp, a certain number of Moss forest species descended into the "Heath forest" to different altitudes, a few even down to 750 m. Above about 900 m. these Moss forest species were so numerous that the "Heath forest" was no longer typical.

At Marudi the "Heath forest" studied occupied a narrow plateau about 1-2 km. from the village. The altitude was only a few metres above sea-level. The greater part of this forest has recently been made into a Government forest reserve in order to preserve the magnificent stand of *Agathis*.

The distribution of "Heath forest" in both places coincided exactly with that of the sandy soil. Thus, in the Koyan valley at about 850 m. there was a small patch of loamy or clayey, not sandy, soil. On this the characteristic "Heath forest" species were absent and there were many strongly buttressed trees; in fact, the forest differed in no important respect from Mixed (Mid-mountain) forest at the same altitude on the Tinjar side of Mt Dulit.

Three soil profiles in the Koyan "Heath forest" were examined:

#### I. *By path between High Camp and Koyan*, altitude about 800 m.

Typical "Heath forest" without *Casuarina*. Litter of dead leaves 2-3 cm. thick. 0-9 cm.: grey-brown, friable mould. (17)<sup>1</sup> 9-38 cm.: grey sand. (18) 38-90 cm.: rather firm, sticky sand, bright yellow, mottled with small grey patches.

#### II. *Near top of sample plot, Koyan valley*, altitude about 750 m.

Typical "Heath forest" with *Casuarina*. Litter of dead leaves 1-2 cm. thick. (12) 0-10 or 15 cm.: chocolate brown, friable mould. (13) 10 or 15-28 or 33 cm.: brownish grey, sticky sand. (14) 28 or 33-60 cm.: lighter coloured, less sticky sand. (15) 60-75 cm.: sticky, brownish grey and black mottled clay.

<sup>1</sup> The numbers in brackets are the reference numbers of the soil samples.

### III. *Near middle of sample plot, Koyan valley, altitude about 750 m.*

Typical "Heath forest" with *Casuarina*. Litter of dead leaves about 2 cm. thick. 0-20 cm.: chocolate brown, friable mould. (10) 20-38 cm.: greyish sand, becoming harder downwards. (11) 38-50 cm.: hard, yellowish, pan-like sandstone.

One profile at Marudi was also examined:

### IV. *Forest Reserve, Marudi, altitude under 50 m.*

Typical "Heath forest" without *Casuarina*. Surface of ground incompletely covered with very thin layer of dead leaves. (33) 0-12 cm.: coarse, loose white sand, with speckled appearance from black humus particles. (34) 12-45 cm.: grey, humus-stained sand in which separate humus particles are not clearly visible to naked eye. (35) 45-75 cm.: loose, pure white sand.

The soil samples gave the following results on analysis:

Profile	No. of sample	Depth cm.	Comber colour	pH	Organic matter %	Moisture at "sticky point" %	Per-centage of sand (1.0-0.04 mm.)	Index of texture
I	17	9-38	Pink on standing	4.7	1.38	18.8	79.5	3
	18	38-90	Pinkish on standing	5.1	0.51	24.3	69.8	10
II	12	0-10 or 15	Colourless	3.9	16.1	Nil	54.5	0
	13	10 or 15-28 or 33	Pale pink on standing	4.4	2.87	21.0	76.3	6
	14	28 or 33-60	Pink on standing	4.7	1.27	21.5	69.2	8
	15	60-75	Pink	3.8	6.66 ?	28.4	27.3	13
III	10	20-38	Colourless	4.4	3.32	22.7	85.0	6
	11	38-50	Faint pink on standing	4.4	5.71	19.9	76.0	5
IV	33	0-12	Colourless	5.8	3.73	Nil	97.8	0
	34	12-45	Colourless	5.9	0.53	Nil	97.8	0
	35	45-75	Colourless	5.6	0.07	Nil	97.8	0

These soils are thus of much lighter texture, especially in the superficial layers, than the Mixed forest soils, though derived from the same rock (sandstone). The Koyan soils are, however, finer grained and richer in colloidal matter (as shown by the "sticky point" determinations) than the Marudi soils. The predominantly pale colours of these soils must indicate intense leaching, and the fact that, though very acid, they all gave feeble or negative reactions to Comber's test, shows that they must be deficient in iron as well as in exchangeable bases.

As might be expected, in all these profiles the humus particles are washed rather deeper than in the Mixed forest profiles. The actual percentages of humus are, however, not much greater than in Mixed forest soils, except in the Koyan profiles, which probably show the effect of the lower temperature due to the higher altitude. The humus particles in "Heath forest" soils tend to be blackish rather than brownish as in Mixed forest soils.



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The soils of the south Bornean "Heath forest" as described by Hackenberg (Diels and Hackenberg, 1926) seem to be very like that of Marudi.

In general character these "Heath forest" soils seem to resemble a European podsol. In a south Bornean profile at a depth of 1.5 m. Hackenberg met with a layer of consolidated, blackened sand 20 cm. thick (1926, p. 302), which perhaps corresponds with a "B" (illuvial) horizon. Possibly a similar layer would have been met with in the Marudi profile if it had been followed deeper.

In both "Heath forest" areas the small forest brooks were "black-water" streams with clear orange-brown water like the "black-water creeks" of British Guiana and other parts of tropical South America. Streams draining the Moss forest also had "black" water, but those draining the Mixed forest always had "white" (colourless) water. The Koyan river itself was a "black-water" stream, so presumably most of its tributaries rose either in "Heath forest" or Moss forest. The Tinjar was a "white-water" river, but some of its small tributaries rising in the Dulit Moss forest carried in some "black" water.

The association of "black-water" with "Heath forest" and white sand soils has also been noticed in several other parts of Borneo. Thus Endert (1925, p. 233) describes an area of white quartz sand in east Borneo (Ulu Mahakam) and says that the natives told him that "black-water" streams always rose on such soils. "Black-water" streams are also found in some parts of Borneo draining the so-called "Waldmoore" or peat swamps, where the soil consists of a great depth of pure raw humus (Polak, 1933).

In the Moraballi Creek area in British Guiana "black-water" streams always rise in the Wallaba forest on the white sand ridges. Presumably the character of the "black" water depends on some common property of the "Heath forest" soils, the very similar Moss forest soils and the peat of the "Waldmoore", not on the nature of the vegetation covering. The "black" colour is no doubt due to humus in a highly dispersed state. Muntz and Marciano examined the water of some South American "black-water" rivers and concluded that the colour was due to "ces acides bruns, mal définis, qui se produisent dans les tourbières" (Muntz and Marciano, 1888, p. 909). The fact that the humus passes out in a highly dispersed condition into the drainage water from white sand and peat swamp soils is perhaps due to the deficiency of these soils in electrolytes capable of flocculating the humus and in clay fractions and iron capable of forming adsorption complexes with it.

### (ii) *Structure and floristic composition*

#### (a) *Upper tree strata.*

No clear-felling plots were made in the "Heath forest", so few data were obtained on the height or stratification of the trees. In a profile view obtained from a hill near Marudi the canopy seemed to be much more level than that of Mixed forest: possibly the first and second storeys of the Mixed forest are represented by a single uneven layer, as in the Mixed forest of British Guiana

(cf. p. 12). The average height of the trees in the canopy at Marudi was roughly estimated at 25–35 m. In most of the Koyan forest it must have been considerably less.



FIG. 6 (a).

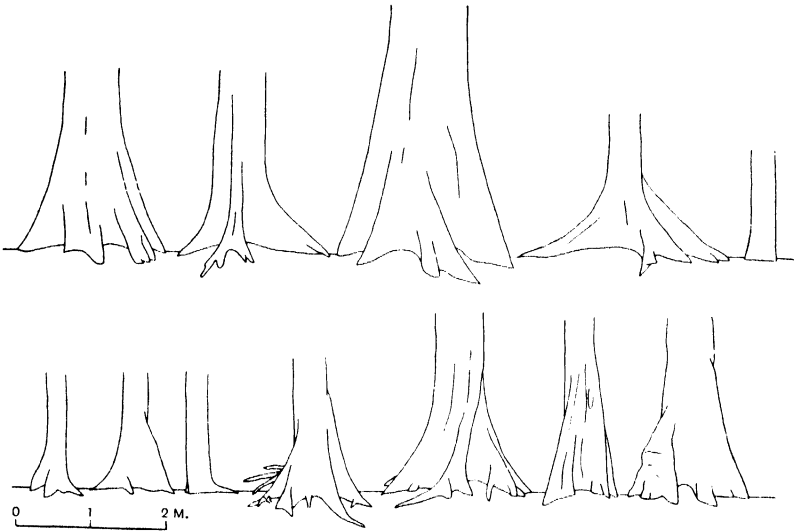


FIG. 6 (b).

FIG. 6. Buttressing of trees in rain forest. (a), side of ridge, Kapah river, Mt Dulit (Mixed forest). (b), summit of ridge, Kapah river, Mt Dulit (Mixed forest). (c), Marudi ("Heath forest"). In (a) and (b) the first twelve, and in (c) the first twenty-four, trees over 8 in. diameter on each side of a straight path are drawn to scale.

As already mentioned, one of the most obvious features of the "Heath forest" is the comparatively slight buttressing of the trees. Not only is there

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a much higher percentage of entirely unbuttressed trees, but where there are buttresses, they tend on the whole to be smaller than in Mixed forest trees. The difference between Mixed forest and "Heath forest" in these respects is brought out very clearly in Fig. 6. Stilt-rooted trees were rather common in the "Heath forest", especially at the Koyan, e.g. *Casuarina sumatrana* Jungh. (R. 1873), and several unidentified species.

The leaves of "Heath forest" trees, especially those in the canopy, are smaller on the average than those of Mixed forest trees: they tend to be thicker and of harder texture. Probably it is for this reason that the canopy of "Heath forest" seen from a distance is of a peculiar dark greyish green tint (almost the colour of olive foliage), quite different from the intense though sombre green of the Mixed forest.

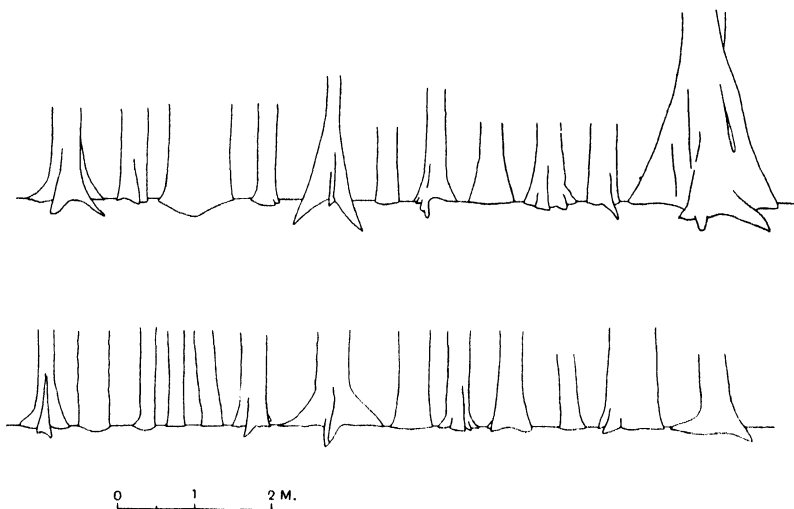


FIG. 6 (c).

Sample plots on which all trees over 8 in. (20 cm.) diameter were enumerated by vernacular names were made both at the Koyan valley and at Marudi Forest Reserve. In each case the plot was 400 ft. (122 m.) square, the same size as the plots in Mixed forest.

The Koyan plot was on very gently sloping ground a few metres from the river bank at an altitude estimated at 750 m. Owing to the depth and narrowness of the valley the situation was very sheltered and somewhat moist.

The Marudi plot was situated at the edge of the sandy plateau. At one corner the ground sloped down rather steeply to a swampy hollow, where the floristic composition differed somewhat from the rest of the plot, but this swampy patch was estimated at one-sixteenth or less of the total area.

The results<sup>1</sup> were as follows:

Diameter class	Number of trees			Totals
	8-16 in. (20-41 cm.)	16-24 in. (41-61 cm.)	Over 24 in. (61 cm.)	
On plot:				
Koyan	238	50	41	329
		91		
Marudi	311	29	10	350
		39		
Per hectare:				
Koyan	168	35	29	232
		64		
Marudi	219	20	7	246
		27		

*Number of "species" (by vernacular names) on plot*

	Trees over 16 in. (41 cm.) diameter	Trees over 8 in. (20 cm.) diameter
Koyan	18	55
Marudi	12	56

The number of trees per unit area is thus about  $1\frac{1}{3}$  times larger in the "Heath forest" plots than in the Mixed forest plot: this difference is probably greater than can be accounted for by the fact that the Mixed forest plot was on a steep slope while the "Heath forest" plots were on comparatively level ground.

In the "Heath forest" of south-east Borneo, "large trunks, which are so frequent in normal forest, occur only isolated" (Winkler, 1914, p. 203). This feature is not apparent on the Koyan plot on which the number of trees in the "16-24 in." class is greater than, and that in the "over 24 in." class equal to, the corresponding numbers on the Mixed forest plot. At Marudi there were slightly more trees in the "16-24 in." class and much fewer in the "over 24 in." class than in the Mixed forest, but the scarcity of very big trees might have been due to artificial depletion, as the plot was not far from a large village. On each plot the number of "species" is much smaller than (a little more than half) that in the Mixed forest plot.

The most abundant tree on the Koyan plot was the conifer, *Dammar minyak* (*Agathis borneensis* Warb., R. 1919), of which there were fifty trees over 8 in. diameter (15.2 per cent. of total) and thirty-two over 16 in. (35.2 per cent. of total). For *Rengas* (Anacardiaceae, *Melanorrhoea* group) the corresponding figures were forty-one (12.4 per cent.) and twenty-eight (30.8 per cent.). A special feature of the plot was the abundance of *Ru rapak* (*Casuarina sumatrana* Jungh., R. 1873), of which there were nineteen (5.7 per cent.) trees over 8 in. and eight (8.8 per cent.) over 16 in. diameter: this species occurred only locally outside the plot. The only other tree forming 5 per cent. or more of the total stand over 8 in. diameter was *Mintangor jangkar* (*Calophyllum* sp.?).

<sup>1</sup> The full results will be found in Appendix II (at end of Part II).

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On the Marudi plot the most abundant tree was not *Agathis* but a Dipterocarp, *Tekam*: of this there were forty-two trees over 8 in. diameter (12.0 per cent. of total) and ten over 16 in. diameter (35.9 per cent. of total). Another Dipterocarp, *Mang* (or *Chengal*), was the next most abundant species and was represented by forty trees over 8 in. (11.4 per cent.), but only one of them was over 16 in. diameter. Of *Agathis* sp.<sup>1</sup> there were thirty-seven trees over 8 in. (10.6 per cent.) and nine over 16 in. (23.1 per cent.). The only other "species" represented by 5 per cent. or over of either the "over 8 in." or "over 16 in." classes were *Orat matah* and *Resak sabut*, both Dipterocarps, and *Ramin* (Anacardiaceae, *Melanorrhoea* group). A marked characteristic of this plot was the gregarious tendency of certain "species"; for instance, patches of *Tekam*, *Resak sabut* and *Bijan laki* were met with.

Both "Heath forest" plots thus resemble one another and differ sharply from the Mixed forest plot in the tendency of certain species to come forward and form a considerable proportion of the total stand. There is thus some approach to the condition of dominance by a single species.

In actual details of floristic composition there is rather a large difference between the two "Heath forest" plots, since there are only seventeen "species" common to both, out of a total of ninety-two "species" on the two. There are many cases, however, of "species" on one plot being represented on the other by other "species" evidently closely related, e.g. *Luis bukit* at the Koyan and *Luis galam* at Marudi, both being probably species of *Hopea*. On neither plot is the floristic composition much like that of the Mixed forest, but the Koyan plot, in this as in some other respects, comes rather closer to it than does the Marudi plot.

The most striking difference between these two "Heath forest" plots is in the proportion of Dipterocarps. At the Koyan they are only feebly represented and are estimated to form only about 5.8 per cent. of trees over 8 in. and 2.2 per cent. of trees over 16 in. diameter. At Marudi they are very strongly dominant as a family, the percentages being 40.5 and 51.3 respectively. The difference is probably related to the difference in altitude between the two plots. The Dipterocarpaceae are a characteristically lowland tropical family and always decrease rapidly in abundance with increasing altitude.

This abundance of a species of *Agathis*, which was a feature of both these sample plots, seems to be typical of Bornean "Heath forest" generally. Winkler (1914) mentions *A. borneensis* Warb. as one of the most characteristic species in the "Heath forest" in south-east Borneo, and in that of south Borneo it is sometimes so abundant that "man kaum mehr von einem Mischwald sprechen kann" (Diels and Hackenberg, 1926, p. 300). In the Dulit district a species of *Agathis* was met with, outside the "Heath forest", only in rocky Mixed (Mid-mountain) forest from 900 to 1100 m. and in small

<sup>1</sup> No specimens were collected, but the species was certainly either *A. borneensis* or the closely allied *A. alba* (Lam.) Foxw.

numbers only: whether this was *A. borneensis* or the closely allied and doubtfully distinct *A. alba* (Lam.) Foxw. was not determined.

*Casuarina sumatrana* Jungh. seems to be a fairly constant and characteristic species in Bornean "Heath forest". It was absent at Marudi, but at Miri (4th Division) it was common in second growth evidently derived from "Heath forest".

*Solunsor* (*Tristania* sp.) is a characteristic tree of "Heath forest" and is conspicuous because of its habit of shedding its bark in long strips which remain attached to the base of the trunk. It occurred on both sample plots, though not in large numbers. According to Hackenberg a species of *Tristania* is abundant in the "Heath forest" of south Borneo (1926, p. 303), but it is curious that Winkler (1914, p. 203) specially mentions the genus as being absent in the "Heath forest" in south-east Borneo, though common in other types of forest. At Mt Dulit species of this genus also occurred in fair abundance in the Moss forest. They were very rare or perhaps quite absent in the Mixed forest.

*Dacrydium elatum* (Roxb.) Wall., which is common in the "Heath forest" of south-east and south Borneo (in the latter locally dominant, according to Hackenberg, 1926, p. 301), was not met with either in the Koyan valley or at Marudi.

(b) *Undergrowth and ground flora.*

One of the most striking characteristics of the "Heath forest" is the thickness of the undergrowth: it is usually difficult to see more than a short distance ahead, and walking about is troublesome unless a path is cut. At the same time the light intensity in the lower levels is obviously higher than in Mixed forest, perhaps because of the smaller size of the leaves of the canopy trees and the scarcity of lianes. No doubt the greater density of the undergrowth depends on the larger amount of light passing through the canopy.

The floristic composition of the undergrowth in the Koyan valley and at Marudi differed considerably. Apart from young trees of taller strata, which were very abundant, the number of species in the undergrowth was relatively small in both places. At Marudi the commonest undergrowth tree was *Podocarpus neriifolius* Don (R. 1006), a species which was abundant on Dulit in the Moss forest, but absent in the Mixed forest. Among the smaller shrubs *Polygala venenox* Juss. ex Poir. sp. (R. 1008) and *Euthemis leucocarpa* Jack (R. 2660) were noted as common and characteristic. The last-named species was also found in the Koyan valley (R. 1870) and appears to be confined to "Heath forest". In the Koyan valley *Pandanus* sp., a genus represented in the Mixed forest only by high epiphytes, was common in the undergrowth.

The herbaceous ground flora of the "Heath forest" is poor in species. At Marudi it consisted almost entirely of orchids (*Plocoglottis Lowii* Rehb. f.,

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R. 2682, and *Coelogyne peltatas* Rehb. f., R. 2657) and ferns (*Lindsaya borneensis* Hk., R. 1009, *Syngamme Lobbiana* (Hk.) J. Sm., R. 2651, *Polypodium Mettenianum* Cesati, R. 2653). In the Koyan valley the number of species was larger, and nearly all of them occurred also in Moss forest or Mixed forest.

Even the ground flora of the "Heath forest" includes species with sclerophyllous foliage, e.g. *Polypodium Mettenianum* Cesati (R. 2653).

Saprophytes are scarce and usually occur as solitary individuals only. The only species seen at Marudi was an orchid. In the Koyan valley the small Liliaceous *Petrosavia stellaris* Becc. (S. 508, R. 1867) was the most frequent saprophyte; it was apparently absent from the Mixed forest.

### (c) *Climbers and epiphytes.*

Winkler (1914) noted in the "Heath forest" of south-east Borneo that lianes were rare and seldom reached arm thickness. The same was true of the Koyan valley and Marudi forests. Small undergrowth climbers, on the other hand, were much commoner than in Mixed forest.

Among these the genus *Nepenthes*, represented by one species, *N. leptochila* Danser (R. 2111), in the Koyan valley, and three, *N. Rafflesiana* Jack (R. 2652), *N. bicalcarata* Hook. f. (R. 2655) and another, at Marudi, is characteristic, occurring, not very abundantly, in damp hollows. This genus is entirely absent in the Mixed forest, and outside "Heath forest" was only seen in Moss forest (where it is represented by different species from those at the Koyan and Marudi) and in certain types of second growth: this distribution suggests that one of the factors excluding these plants from the Mixed forest is probably the deep shade in the undergrowth.

Epiphytes grow at much lower levels in "Heath forest" than in Mixed forest. Species which in the latter are found mainly in the tree tops and rarely, if ever, descend below about 12 m., may be found in the latter at heights only 1–3 m., or even occasionally on the ground itself. Some examples noted at Marudi were *Drynaria quercifolia* (L.) J. Sm. on a trunk at 0.5–1.5 m. (Marudi), *Humata repens* (L. f.) Diels (R. 2681), not uncommon at bases of trunks and on the ground, and *Asplenium nidus* L. on the ground. At Marudi one of the Loranthaceae (*Macrosolen Beccarii* Becc.?, R. 2680) occurs as a parasite on shrubs and small undergrowth trees: in the Mixed forest this family is almost confined to the crowns of first-storey trees, except in openings. Several species of orchids were also common at heights of 0–3 m. from the ground, both at the Koyan and Marudi: in Mixed forest orchids were rare except in the tops of tall trees. The "Heath forest" appears to be much richer in epiphytes than the Mixed forest, but this may be chiefly because they are more easily seen: there are, however, in addition to most of the Mixed forest epiphytes some species which seem to be peculiar to the "Heath forest". Since the sun epiphyte society descends so low, there is very little room left for a shade

epiphyte society: it is limited to those trees which happen to be particularly well shaded by their neighbours.

Bryophytes are much more abundant in the "Heath forest" than in the Mixed forest, and not only are epiphytic species abundant on the undergrowth, but a few species are not uncommon on the ground, e.g. *Leucobryum javense* (Brid.) Mitt. (R. 2663) and *Leucophanes candidum* Brid. (R. 2665), which sometimes form extensive carpets: as already mentioned, in the Mixed forest mosses occur only exceptionally on the ground, except above 450 m.

### (iii) *Distribution and relation to other types of vegetation*

The "Heath forest" association seems to be widespread in Borneo. In Sarawak as well as at the Koyan valley and Marudi it is no doubt present near Miri (4th Division), where a large area of second growth was seen which was evidently derived from it. In parts of southern Sarawak (Siul, near Kuching and near Marop on the Batang Lupar) Beccari met with small areas where the vegetation differed from the surrounding forest (Beccari, 1877 and 1904, p. 215): the soil of these areas was "a white crystalline sand" (Beccari, 1904, p. 147), and among the characteristic plants mentioned are *Dacrydium elatum* (Roxb.) Wall., *Casuarina sumatrana* Jungh. and *Nepenthes* spp. There can be little doubt that the areas in question were small patches of "Heath forest". According to Beccari, the Malays called them *mattang* (= ridges) and looked on them as haunted by spirits. Beccari himself held that they were "islands at a time when the surrounding plain had not yet emerged from the sea" (1877, p. 215, Transl.) on which the vegetation had persisted unchanged.<sup>1</sup>

In Dutch territory "Heath forest" has been described from South-east Borneo by Winkler (1914) and from South Borneo by Diels and Hackenberg (1926). In West Borneo Beccari found "mattangs" and "black-water" rivers on the Umpanang (Ulu Kapuas): Hallier also speaks of forests reminiscent of those of Australia (quoted in Winkler, 1914, p. 202) in that Residency.

In East Borneo Endert met with a type of forest on white sand, which, to judge from his account, must have been secondary forest derived from "Heath forest". In it *Tristania obovata* R.Br. and other Myrtaceae were abundant, while *Casuarina* sp. and *Dacrydium elatum* (Roxb.) Wall. also occurred (Endert, 1925, p. 232).

As Winkler points out, "Heath forest" has little in common with Monsoon forest. Characteristic Monsoon forest trees such as *Tectona* spp. are wanting and the proportion of deciduous trees is probably not larger than in the Mixed forest.

Though very unlike in general appearance "Heath forest" resembles Moss

<sup>1</sup> Curiously **Spruce** (1908, p. 354) also looked on the *caatinga* forests of the Rio Negro as relics of an ancient and now vanishing type of vegetation. These *caatingas* are similar to the Guiana Wallaba forests (**Davis** and **Richards**, Part II, p. 126) which, as will be shown, are closely analogous to "Heath forest".



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forest in certain respects and differs from it less widely than does Mixed forest. These resemblances may be tabulated as follows:

Moss forest	"Heath forest"	Mixed forest
Lower levels usually well illuminated	Lower levels usually well illuminated	Lower levels deeply shaded
Undergrowth dense	Undergrowth dense	Undergrowth thin
Ground flora scanty	Ground flora poor in species	Ground flora moderately rich in species
Bryophytes very abundant at lower levels	Bryophytes rather abundant at lower levels	Bryophytes not abundant
No buttressed trees	Buttressed trees comparatively uncommon	Buttressed trees abundant
Conifers abundant	Conifers common	Conifers absent
<i>Casuarina sumatrana</i> present	<i>Casuarina sumatrana</i> present	<i>Casuarina sumatrana</i> absent
<i>Tristania</i> spp. frequent	<i>Tristania</i> sp. frequent	<i>Tristania</i> sp. absent or rare

Since Mixed and "Heath forest" live under similar, and Moss forest under quite different climatic conditions, the resemblances between the two latter must depend on similarity of soil: "Heath" and Moss forest soils are in fact much alike (cf. pp. 24 *et seq.* and Part II).

Similarity of soil and good illumination probably account for the fact referred to above (p. 24) that mountain species descend to much lower altitudes in "Heath forests" and on sandy soils in general, than in Mixed forests and on heavy soils. Examples of this phenomenon are seen among the following ferns, conifers and angiosperms.

*FERNS.* *Cyathea recommutata* Copel. (R. 1638). Abundant in Dulit Moss forest and in Koyan "Heath forest" down to at least 750 m. Absent in Mixed forest even above 800 m.

*Oleandra oblanceolata* Copel. (R. 1668). Common in Dulit Moss forest and frequent in Koyan "Heath forest" to at least 750 m. In Mixed forest not below c. 960 m., except for one plant which was seen at c. 900 m. as an epiphyte at c. 10-15 m. above the ground.

*Dipteris conjugata* Reinw. (R. 1635). In Dulit district confined to Moss forest; in Moss forest on most Sarawak mountains. In "mattangs" in plain near Kuching, according to Beccari (1904, p. 16). One other lowland record from Sarawak known to me: moist rocks, Lawas R., Burbidge in Kew Herb.

*Matonia pectinata* R.Br. (the Dulit, and probably all the Sarawak specimens belong to the geographical race, *M. Foxworthyi* Copel). In the Dulit district confined to Moss forest (R. 1626), but found in "mattangs" in plain near Kuching, according to Beccari (1904, p. 16).

*CONIFERS.* *Podocarpus neriiifolius* Don. See p. 31.

*Phyllocladus hypophylla* Hook. f. Abundant in Dulit Moss forest (R. 1058, etc.) and stopping sharply at boundary of the Mixed forest. Occasional in Koyan "Heath forest" down to at least 750 m. The tallest specimen seen (14.8 m. high) at the lowest altitude.

*Dacrydium elatum* (Roxb.) Wall. Common in Moss forest on Dulit, etc. (R. 1059, etc.). Absent in Mixed forest in Dulit district. In "mattangs" in plain near Kuching (Beccari, 1904, p. 16); in "Heath forest" on the plain in South-east Borneo (Winkler, 1914, p. 203) and South Borneo (Diels and Hackenberg, 1926, p. 301).

*Agathis*. See p. 30.

**ANGIOSPERMS.** *Styphelia malayana* (Jack) J. J. Sm. In Dulit district in Moss forest at c. 1230 m. (R. 1619): absent in Mixed forest. Widespread in Moss forest in the Malayan region, also a number of records in the lowlands; where data are available, these lowland localities seem to be on sandy soil (cf. van Steenis, 1933, p. 52), thus No. 28708 in Herb. F.M.S. For. Res. Inst., from Ulu Tutong, Brunei, is labelled "on white sand ridge in plain".

Van Steenis (1933) has recently given a discussion of the occurrence of Malayan mountain plants at low altitudes with special reference to the plains of Sumatra and has concluded that, (i) lowland stations for mountain species usually have relatively open vegetation and frequently sandy soil, (ii) the mountain species which descend to low altitudes always belong to eurytherm genera: members of truly stenotherm genera such as *Gentiana*, *Juncus*, etc., never descend below 1000 m. The facts just given are thus in agreement with these conclusions.

From the above account it is evident that "Heath forest" is a type of primary rain forest determined by special local soil conditions. If Clements' system of vegetation classification is followed strictly it should probably be considered a preclimax type. Such a view, however, would seem to force the facts into an artificial scheme, for as no change of conditions can be imagined which would convert a "Heath forest" soil into a Mixed forest soil, no succession actual or potential is involved in the relation of the two types of forest.<sup>1</sup> It is therefore much more natural to look on "Heath forest" as an "edaphic climax" in the sense of Tansley and others.

It must by now be evident that there is a remarkably close resemblance in both structure and floristic composition between the Bornean "Heath forest" and the Wallaba forest of British Guiana (Davis and Richards, Part II, pp. 122-6). The differences between the "Heath" and Mixed forest types of Mt Dulit are almost all analogous to the differences between the Wallaba and the Mixed forest types of Moraballi Creek.

In Borneo the tendency towards dominance is much less pronounced, as the most abundant tree on the two sample plots of "Heath forest" formed only 12 and 15 per cent. respectively of all trees over 8 in. diameter,<sup>2</sup> while in

<sup>1</sup> It is conceivable, however, that the "Heath forest" soil may be produced from the Mixed forest soil by some kind of differential erosion: if that could be established, "Heath forest" would presumably have to be regarded as the climax and Mixed forest as a subclimax, or "Heath forest" as a *post-climax* and Mixed forest as the *climax*.

<sup>2</sup> Dominance is, however, greater in the "Heath forest" of South Borneo, see above, p. 30.

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Wallaba forest the corresponding percentage for the dominant species was 26, but even the Mixed type in British Guiana shows a certain tendency towards dominance. The actual species in "Heath forest" and Wallaba forest are, of course, totally different. The Wallaba forest is dominated by Leguminosae, which are only sparingly present in "Heath forest", and it contains no conifers. The resemblance between the two types is, however, very far reaching and extends even to those indefinable characteristics summed up as the "general aspect" of the forest. Indeed, it is hardly exaggerating to say that in many parts of the "Heath forest" it was as if every individual plant in the Wallaba forest had been replaced by one of similar habit and general appearance but of different systematic affinities.

This resemblance, no doubt, depends on similarity of soil and climate. The Marudi soil profile in particular is extremely like the Wallaba forest profile (Davis and Richards, Part II, pp. 123-4).

Whatever conclusion is reached as to the status (preclimax or edaphic climax) of "Heath forest" will clearly apply equally to Wallaba forest, and *vice versa*.

The most important points of analogy may be recapitulated as follows:

BORNEO	GUIANA
"Heath forest" differs from Mixed forest in:	Wallaba forest differs from Mixed forest in:
(1) Larger number of trees per unit area.	
(2) Smaller amount of buttressing of trees.	
(3) Better illumination of lower levels.	
(4) Denser undergrowth.	
(5) Smaller number of species of ground herbs.	
(6) Scarcity of large lianes.	
(7) Tendency of epiphytes to grow at lower levels.	
(8) Tendency towards the dominance of a single species of tree.	

#### REFERENCES

- Airy-Shaw, H. K.** "Studies in the Ericales. II. A new genus of Vaccinioideae from Borneo." *Kew Bull.* pp. 150-6, 1935.
- Beccari, O.** *Malesia*, 1. Genoa, 1877.
- Beccari, O.** *Wanderings in the great forests of Borneo*. Edited by F. H. H. Guillemard. London, 1904.
- Brown, W. H.** "Vegetation of Philippine Mountains." *Dept. of Agric. and Nat. Resources, Bur. of Science, Manila*, Publ. 13, 1919.
- Carr, C. E.** "Some Malayan orchids." *Gdus' Bull. Straits Settlements*, 8, 69-129, 1935.
- Danser, B. H.** "The Loranthaceae of the Oxford Expedition to Sarawak in 1932." *Rec. Trav. bot. néerland.* 31, 237-47, 1934.
- Davis, T. A. W. and Richards, P. W.** "The vegetation of Moraballi Creek, British Guiana: an ecological study of a limited area of tropical rain forest." Part I, This JOURNAL, 21, 350-84, 1933; Part II, *Ibid.* 22, 106-55, 1934.
- Diels, L. and Hackenberg, C.** "Beiträge zur Vegetationskunde und Floristik von Süd-Borneo." *Bot. Jb.* 60, 293-316, 1926.
- Dixon, H. N.** "A contribution to the moss flora of Borneo." *Journ. Linn. Soc. (Bot.)* 50, 57-140, 1935.
- Endert, F. H.** *Verslag van de Midden-Oost-Borneo Expeditie*. Batavia, 1925.
- Foxworthy, F. W.** "Commercial timber trees of the Malay Peninsula." *Malay. For. Rec.* 3, 1927.

- Giesenhagen, K.** "Die Moostypen der Regenwälder." *Ann. Jard. Bot. Buitenz.* Suppl. **3**, 711-90, 1910.
- Harrison, T. H.** "The Oxford University Expedition to Sarawak 1932." *Geogr. J.* **82**, 385-410, 1933.
- McLean, R. C.** "Studies in the ecology of tropical rain forest: with special reference to the forests of South Brazil." *This JOURN.* **7**, 5-54 and 121-72, 1919.
- Martin, F. J. and Doyne, H. C.** "Laterite and lateritic soils in Sierra Leone." *J. Agric. Sci.* **17**, 530-7, 1927.
- Muntz, A. and Marciano, V.** "Sur les eaux noires des régions équatoriales." *C.R. Acad. Sci.* Paris, **107**, 908-9, 1888.
- Polak, E.** "Über Torf und Moor in Niederländisch Indien." *Verh. kon. Akad. Wet. Amst.* 2de sectie, **30**, No. 3, 1933.
- "Rainfall in Sarawak." *Sarawak Mus. J.* **4**, 219-21, 1933.
- Spruce, R.** *Notes of a botanist on the Amazon and Andes*, **2**. Edited by A. R. Wallace. London, 1908.
- Symington, C. F.** "Notes on Malayan Dipterocarpaceae. II." *Gdns' Bull. Straits Settlements*, **8**, 1-40, 1934.
- Uttien, H.** "The Cyperaceae of the Oxford University Expedition to Sarawak in 1932." *Rec. Trav. bot. néerland.* **32**, 193-202, 1935.
- van Steenis, C. G. G. J.** "Report of a botanical trip to the Ranau region, South Sumatra." *Bull. Jard. Bot. Buitenz.* Ser. 3, **13**, 1-56, 1933.
- Whitford, H. N.** "Composition and volume of Dipterocarp forests in the Philippines." *Philippine J. Sci.* **4**, 699-725, 1909.
- Winkler, H.** "Die Pflanzendecke Südost-Borneos: Beiträge zur Kenntnis der Flora und Pflanzengeographie von Borneo. IV." *Bot. Jb.* **50**, 188-208, 1914.

# CONTRIBUTIONS TO THE AUTECOLOGY OF *MERCURIALIS PERENNIS* L.

BY THE LATE S. K. MUKERJI, D.Sc. (LOND.)

(With three Figures in the Text)

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## INTRODUCTION

THE present publication is the result of investigations carried out in 1926 and 1927 under the supervision of Dr (now Professor) E. J. Salisbury at University College, London, with a view to gaining some knowledge of the autecology of *Mercurialis perennis* L., especially with respect to its soil requirements in Britain.

The elucidation of the facts ascertained in regard to distribution on soils of various types led to further investigations respecting the geographical distribution not only of this species but of the entire genus *Mercurialis*; the part played by light intensity in governing the distribution and growth of the male and female plants of *M. perennis* in woodlands and the competition between male and female plants of the same species; the causes of the rare occurrence of seedlings in nature and the conditions necessary for the germination of the seeds. The osmotic pressures and the pH gradients of the sap of the plant, the hydrogen-ion concentration of the soil in relation to the wilting coefficient and the growth of roots and shoots were also studied.

In contrast to the large amount of synecological work that has been published during the last two or three decades, our knowledge of the autecology, even of the commonest species, is still very meagre, and the time has now come when the conditions which determine the occurrence, growth, and reproduction of the more characteristic species of the diverse types of plant communities in nature should be studied in detail, if any real progress in synecology is to be made.

Works dealing with the morphology, biology and autecology of the dog's mercury are far less numerous than might be supposed, when its very widespread occurrence in Europe and its frequent dominance of the ground vegetation of different types of woodlands in Britain and on the continent are considered. Except for short studies by Winkler (1880), Hegi (1931), and an account recently published by Gillot (1925), bearing on certain aspects of the chemistry and biology of this species, and such relevant observations and remarks as are embodied in autecological studies of other species and in synecological studies of British woodlands (e.g. by Woodhead (1906), Adamson (1912), Salisbury (1916, 1918, etc.), Tansley (1917), and Watt (1923)), there is very little information available. The present paper is therefore an attempt partially to bridge this gulf in our knowledge of this plant, at any rate in certain directions.

The author is deeply indebted to Dr E. J. Salisbury for his keen and constant interest, valuable suggestions and advice, and to Prof. F. W. Oliver for numerous facilities during the progress of the work. He also wishes to thank the authorities of the Herbaria at Kew, the British Museum, and the Botanical Institutes at Vienna and Berlin, for facilities in the consultation of herbarium specimens and museum collections. He is also indebted to Mr W. Hales of the

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Chelsea Physic Garden for the culture of some of his specimens, to Dr A. B. Rendle of the British Museum and to Messrs W. B. Turrill and T. A. Sprague of Kew for their helpful criticisms in connection with the description of a new variety of *M. perennis* (var. *Salisburyana*), which was discovered at Staplehurst in Kent in the year 1926.

### HABITATS

*M. perennis* L. is a gregarious herbaceous plant. In nature it usually grows in dense masses often as one of the principal herbaceous elements of the ground flora of beech, oak, ash, elm and other types of woodlands in Europe. It also occurs under the shade of hedgerows and scrub. It is, by nature, a shade-loving plant, manifesting a decided preference for moderately shady to densely shady habitats. Under such conditions, the plants, especially the females, are very vigorous and often display a darker green colour. But under conditions of strong insolation *M. perennis* is capable of continued existence, at any rate for some time, though with much abated vigour.

The ultimate period of subaerial vegetative and reproductive activity depends upon a number of factors, of which illumination is one, but soil reaction, soil moisture, etc., dealt with in detail in subsequent parts of this paper, also affect its duration.

*M. perennis* appears to have an extensive range with regard to the type of soil on which it will grow. It occurs, for instance, on sandy soils, as at Westerham, on heavier clays and clayey loams, as at Staplehurst, on marls, loams and lighter soils, as at Chiselhurst and Orpington (all in Kent), on chalk and clay with flints, as at Boxhill and Woldingham (Surrey), and lastly on the soil of older igneous and siliceous rocks, for it is often found to be a dominant constituent of the undergrowth of deciduous woods on granite and schist in Scotland. Although it is fairly common on dark-coloured humus as at Purley Beeches (Surrey) and in Epping Forest (Essex), it is extremely rare on peat.

Such a diversity of soil types indicates that soil texture is relatively unimportant as far as the distribution of *M. perennis* in nature is concerned, though this factor is of some consequence in affecting its degree of development and growth.

The scarcity of the species and sometimes its total absence on the raw soils of newly formed habitats is strikingly noticeable, just as its preference for the older ones where the top few inches of the soil have a high organic content, as in old woodlands, is distinctly manifest.

Altitudinally *M. perennis* extends from sea-level to a considerable elevation on mountains. The ultimate height attained in different mountainous regions, e.g. in Scotland, England, Germany and Switzerland, naturally varies in accordance with the latitude and other geographical factors. For instance, in the Lake District of England, it extends from the level of the lakes to an

altitude of about 400 m. on the adjoining hills, while in Central Europe it occurs on the Alps up to elevations ranging from 1600 to 2000 m.

#### COMMON ASSOCIATES

The principal types of woodlands with which *M. perennis* is associated in Britain are Fagetum silvaticae, Quercetum roboris and Fraxinetum excelsioris. It also forms a feature of the damper areas and flushes of the Quercetum sessiliflorae and of the Alnetum glutinosae. And again, it occurs in woods and copses dominated by *Ulmus*, *Betula*, *Taxus*, *Pinus*, *Buxus*, *Carpinus* and *Tilia*.

The commoner shrubs with which it is associated are *Salix* (*atrocinerea*, and *Caprea*), *Juniperus*, *Corylus*, *Carpinus*, *Rhamnus catharticus*, and species of *Rosa*.

Among herbaceous species, there is a fairly large number of plants which grow in close association with *Mercurialis perennis* in nature. In Britain it is commonly associated with the following among others:

<i>Allium ursinum</i>	<i>Euphorbia amygdaloides</i>	<i>Glechoma hederacea</i>
<i>Arum maculatum</i>	<i>Ficaria verna</i>	<i>Primula acaulis</i>
<i>Asperula odorata</i>	<i>Filipendula ulmaria</i>	<i>Scilla nutans</i>
<i>Deschampsia caespitosa</i>	<i>Galium</i> spp.	<i>Viola</i> spp.

#### PART I. TAXONOMY AND DISTRIBUTION OF THE GENUS *MERCURIALIS*

##### SYNOPSIS

The genus *Mercurialis* belongs to the family Euphorbiaceae and to the subfamily Crotonoideae. It is included in the tribe Acalyphae, which is characterised by spiked, racemed or paniced inflorescences and also by the lack of any laticiferous tissue, in the place of which tanniferous cells (or tissue) are sometimes found.

According to Pax (1914) there are three other genera closely allied to *Mercurialis*, viz. *Seidelia*, *Leidesia* and *Dysopsis*, the distinctions between these being based on the characters of the calyx and stamens:

Stamina pauca vel numerosa. Ovarii rudimentum nullum. Discus nullus, nullus vel rarius evolutus. Plantae herbaceae.

##### A. Calyx per anthesin tripartitus.

###### (a) Calyx evolutus.

Stamina 8-20. Folia opposita.

Stamina 2-5. Folia alterna, infima opposita.

###### (b) Calyx nullus vel ad bracteam unicam reductus.

##### B. Calyx urceolaris, trifidus.

46. *Mercurialis* L.

47. *Seidelia* Baill.

48. *Leidesia* Mull. Arg.

49. *Dysopsis* Baill.

The genus *Mercurialis* itself consists of nine species (but see pp. 48-51) and the main taxonomic characters used in distinguishing them are the type of inflorescence, the annual or perennial habit, and the glabrous or hairy condition of the vegetative organs, but chiefly the ovary and the capsule, the woody or herbaceous nature of the plant, and lastly the character of the



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lamina. This will be evident from the following "*Clavis specierum*" of Pax (1914):

### A. Flores fasciculati.

#### (a) Species perennes; caulis inferne lignescens.

Ovarium dense vestitum.

##### I. Planta albo-tomentosa.

1. *M. tomentosa*.

##### II. Planta mox omnino glabrescens.

2. *M. Reverchonii*.

Ovarium glabrum.

##### I. Semina laevia (species hispanica et maroccana).

3. *M. elliptica*.

##### II. Semina foveolata (species corsica et sardinica).

4. *M. corsica*.

#### (b) Species annuae. Ovarium vestitum et muricatum. Planta glabrata. 5. *M. annua*.

### B. Flores in inflorescentiam spiciformam dispositi.

#### (a) Ovarium vestitum. Capsula pubescens (species europaeae).

Folia petiolata, ovatolanceolata vel lanceolata.

6. *M. perennis*.

Folia sessilia vel subsessilia, late ovata.

7. *M. ovata*.

#### (b) Ovarium glabrum. Capsula glabra vel parcissime setosa, muricata. 8. *M. leiocarpa*.<sup>1</sup>

## VARIETIES AND HABITAT FORMS

*M. perennis* exhibits considerable variation in some of its morphological characters. This is specially noticeable in the outline, shape and hairiness of its leaves, in the size of the lower leaves, in the number of stamens, and in the size of the seeds and fruits. These variations are of two types, first those which breed true and secondly those which are not fixed but are liable to change under conditions of cultivation. Keeping these points in view, *M. perennis* may be said to possess three distinct varieties and at least six habitat forms.

The three varieties are:

(1) *M. perennis* L. var. *genuina* Müller-Aarg: "mit breitelliptischen Laubblättern, nur 2—bis 3—mal so langen als breiten, oberseits fast kahlen, unterseits an den Seitennerven sehr spärlich und höchstens auf den Mittelnerven behaart" (Hegi, 1931).

(2) *M. perennis* L. var. *Salisburyana* Mukerji (Mukerji, 1927). This new variety of *M. perennis* was discovered in March 1926 at Staplehurst (Kent). It differs from the type in the following respects:

- (a) deeply serrated leaf margin (recalling the leaves of *Urtica dioica*),
- (b) generally shorter petiole,
- (c) darker green colour,
- (d) more hispid character, and
- (e) generally shorter and upwardly directed stigmas.

(3) *M. perennis* L. var. *leiocarpa* Mukerji (syn. *M. leiocarpa* Sieb. et Zucc.). See below pp. 47, 48, 50, 51. The Far Eastern species of *Mercurialis*—viz. *M. leiocarpa* Sieb. et Zucc.—has been shown by me as the result of a careful and detailed examination of all the herbarium specimens of the genus *Mercurialis*

<sup>1</sup> Here reduced to a variety of *M. perennis* (see below).

preserved in the herbaria at Kew, the British Museum and the Edinburgh Museum, to be nothing more than a variety of *M. perennis* L.

Besides these three varieties of *M. perennis* the following six habitat forms may be distinguished in nature:

(a) f. *silvatica* (Hoppe s. str.). Leaves very much elongated, elliptic-lanceolate, pointed. Mid-nerve and veins of the leaves usually very much thicker than those of the type.

(b) f. *ovatifolia* (Hausskn.). Leaves ovate to ovate-lanceolate, upper part of the stem above the middle region generally hanging down. Petiole decidedly shorter than in the type. This form grows on sunny slopes in bushes and thickets or on entirely exposed dry situations.

(c) f. *angustifolia* (Murr.). Grows, like the preceding, in sunny situations, but the leaves are comparatively narrow and lanceolate, more hairy and thicker than in the type.

(d) f. *robusta* (Gross). Leaves unusually large, 10–15 cm. long, and over 5 cm. broad. Seeds 4–5 mm. long. Plants very much taller and more robust than the type, sometimes attaining a height of about 60–65 cm. Generally under old oak or beech in fairly damp and shady localities.

(e) f. *saxicola* (Beck.). Leaves elongate-elliptic, 4–5 times as long as broad, gradually tapering towards the apex. Both the upper and lower faces of the leaves more hairy than in the type. Generally on exposed chalky hills.

(f) f. *variegata* (Mukerji). Besides the above-mentioned habitat forms there is an ecad which bears well-marked variegated leaves, and this I propose to call f. *variegata*. Its leaves possess beautiful mottled patches of yellow and white, and by continued cultivation this may be further improved. Some day it may perhaps find favour with gardening enthusiasts.

The significance of these various types will be appreciated when we come to consider the leaf forms of male and female plants (see p. 72) and the diversity of leaf form in the individual plant itself (see p. 70).

#### GEOGRAPHICAL DISTRIBUTION OF THE GENUS *MERCURIALIS*

The genus *Mercurialis* consists of nine species, of which as many as seven are found in Europe and in the adjoining Mediterranean region, while the remaining two species, viz. *M. leiocarpa* Sieb. et Zucc., and *M. transmorrissonensis* Hayata, are isolated from the rest, being restricted to the eastern Asiatic region (see map, p. 49).

Thus from the phyto-geographical standpoint, two broad divisions, the Western group and the Far Eastern group, may be recognised, into which all the species of *Mercurialis* can be placed.

These two principal groups in their turn show well-marked centres of distribution. The Western group may be further subdivided into the Mediterranean subgroup and the Central European subgroup.

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### (i) *Western group*

This group comprises an assemblage of species which exhibit a great diversity of ecological types, ranging from such pronounced xerophytic forms as *M. tomentosa* to completely mesophytic forms like *M. perennis*. Some species possess remarkable powers of withstanding drought and are capable of existing under conditions of severe exposure to wind and insolation. They normally grow in rocky mountainous areas and in the desert regions of Morocco and Spain, in contrast to the species which can only grow in humid shady and sheltered localities. These latter cannot exist under conditions of drought or in situations exposed to wind and insolation. Both annuals as well as perennials are included in this group.

Out of the seven species which make up this group, the following five belong to the Mediterranean region: *M. elliptica*, *M. Reverchonii*, *M. Corsica*, *M. tomentosa* and *M. annua*, while the two remaining species, *M. perennis* and *M. ovata*, have their centres of development in Central Europe.

#### (a) *Mediterranean subgroup.*

This includes most of the species. *M. elliptica* and *M. Reverchonii* are restricted to the south of Spain and the opposite north coast of Africa. *M. Corsica* is an endemic species confined to the islands of Corsica and Sardinia. *M. tomentosa*, which is a pronounced xerophyte, occurs in Spain, France and certain parts of the Balkan Peninsula and Central Europe. Lastly comes *M. annua*, a small ruderal annual which has a very wide range of distribution, occurring not only throughout the Mediterranean region, but practically all over Europe, and even over a great portion of the Near East.

Besides the species of the Mediterranean subgroup, other species, like *M. perennis*, which is normally a member of the Central European subgroup, have their southern limits of distribution in the Mediterranean region. Hence there results a certain amount of overlapping in the areas of distribution of certain species which are typically members of one subgroup or another.

The characters, habitats and distribution of the Mediterranean species are briefly as follows:

(1) *M. elliptica* is a perennial, more or less glabrous, suffruticose herb, 30–50 cm. high, which grows on stony and rocky ground and in waste land. It is rather restricted in distribution, occurring only in the southern part of Spain, in Portugal and in Morocco. It is also found, though rarely, in the small island of Minorca. On account of its close resemblance to *M. corsica*, it has sometimes been confused with the latter, and the differences require further investigation.

(2) *M. Reverchonii* is a perennial much-branched suffruticose herb, 30–60 cm. high, the young parts of which are pubescent and the older more or less glabrous. This species often grows in association with *M. elliptica* on rocky ground in southern Spain and in Morocco. Like the preceding, its centre of

distribution also lies in the south-western Mediterranean region. It occurs in Spain from Sierra de Palma to Algeciras, and is fairly abundant in the mountainous areas near Tetuan in Morocco.

(3) *M. Corsica* is a branched perennial suffrutescent herb, 30–60 cm. high, which grows in bushland, along roadsides in shady situations, and also in mountainous regions. According to Pax (1914) and Hegi (1931) it is an endemic species confined to the islands of Corsica and Sardinia. But of this I am rather doubtful, for on the strength of my study of the genus I believe that some day it may be reported from the mainland of Europe. As stated above, the relationship of this species to *M. elliptica* requires further careful taxonomic examination, for *M. Corsica* may be no more than a variety of *M. elliptica*.

(4) *M. tomentosa* is a much-branched bushy form, 30–75 cm. high. It is conspicuous by its white woolly covering. It grows in all kinds of dry situations such as waste-land areas, roadsides, and on rocky and stony ground. Its centre of distribution lies in south-eastern Spain and southern France, extending to the western coast of Italy. It is sparsely represented in some of the western parts of the Balkan Peninsula and also occurs, though rarely, in parts of the Central European region. It is a pronounced xerophyte and, unlike the members of the Central European subgroup, viz. *M. perennis* and *M. ovata*, can withstand prolonged desiccation and exposure to a remarkable degree.

(5) *M. annua* is a branched annual herb, 20–40 cm. high, which grows as a ruderal plant in waste-land areas, along roadsides and hedgebanks, and also as a weed of cultivation in fields and gardens.

Of all the species of *Mercurialis*, *M. annua* appears to be the most widely distributed. It extends from England in the west to the Caucasus, western Siberia, Chinese Turkestan and Persia in the east, and from Belgium, northern Germany and mid-Russia in the north to the north coast of Africa, Egypt, Macedonia and Asia Minor in the south. Besides its normal distribution in the areas mentioned above, *M. annua* is also reported as introduced to a varying extent in several parts of the world, including the West Indies, Cape Colony, and some of the smaller islands off the west coast of Africa, such as Madeira and the Canary Islands (cf. Hegi, 1931; Pax, 1914).

It is definitely recorded from the following areas: Britain (where it is believed to be indigenous in England including the Isle of Wight but not in Scotland and Ireland), France, Spain, Portugal, Belgium, Germany, Switzerland, Tirol, Austria, Hungary, Czechoslovakia, Roumania, Bulgaria, Yugoslavia, Turkey, mid-Russia, Caucasus, Chinese Turkestan, Persia, Syria, Palestine, Italy, Sicily, Corfu, Albania, Greece (Macedonia), Crete, Smyrna, Morocco, Algeria, Tripoli, Egypt.

(b) *Central European subgroup.*

The two main species which constitute this subgroup are *M. perennis* and *M. ovata*. Besides these, there is a certain amount of overlapping of other

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species in this region, which is due to the northern extension of certain members of the Mediterranean subgroup such as *M. annua* and *M. tomentosa*.

(6) *M. perennis* may be said to be the most important member of the Central European subgroup, as it certainly appears to have attained its greatest development in this region. In the south-eastern parts of its area, *M. perennis* has probably given rise to another member of the same subgroup, viz. *M. ovata*. There is a very close resemblance in external morphological characters, so much so that Hegi (1931) mentions that they have been at times placed by mistake under the same heading by different workers. I am also inclined to think that, as in the case of *M. Corsica*, *M. ovata* requires further critical study before the question of its identity and specific rank can be finally settled one way or the other. From a close examination of the herbarium material at Kew and the British Museum it looks as if the specific rank of *M. ovata* is not perhaps very secure.

As stated above, *M. perennis* occurs over the whole of Central Europe, being sometimes associated with *M. annua* and *M. ovata*. It extends far and wide, even beyond the boundaries of Europe. Eastwards it is reported from the Caucasus to Persia (Hegi, 1931); on the south, in the Balkan Peninsula and the north African region. On the west it grows abundantly in England and Scotland, but less so in Ireland which is its western limit of distribution. Northwards it extends to southern Norway, mid-Sweden, northern Germany and northern Russia, but not to the extreme north. In Central Europe it occurs in several kinds of woodland but especially in beechwoods. Generally speaking, wherever it is present, it may be frequent to very abundant. It extends from the plains to the subalpine regions but is rather scantily represented in the subarctic region.

Occasionally, it may be entirely absent or very rare indeed over extensive areas. For example, in Germany, although abundantly distributed in the north-eastern parts, it is rare in the north-western areas; and is in fact definitely reported to be absent from a number of localities, e.g. from Cleve, Wessel and in the pure oak forests of western Schleswig-Holstein, and from the islands in the North Sea.

In Austria and Switzerland it is very common, but on the other hand almost entirely absent from the central alpine valleys such as those of the Engadine and others. Though fairly widely distributed in France, it is restricted in its distribution in Spain where it is believed to be confined chiefly to the north-eastern parts.

In its southern extension it overlaps the areas of distribution of the typical Mediterranean forms, being generally distributed over the whole of southern Europe including the Balkan Peninsula and the islands of Corsica and Sicily.

Finally it may be pointed out that it is said to have been introduced in certain parts of Australia.

*Altitudinal distribution of Mercurialis perennis* L. In the British Isles this species has been reported from hilly stations up to an elevation of 300–400 m. In Switzerland it extends to an altitude of about 2000 m. (more than 6500 ft.), in Tirol to 1800 m. only, while in Austria it does not generally occur above 1600 m. In Germany, e.g. in Bavaria, its altitudinal range is still lower, being somewhere about 1200 m.; while in Belgium 500–700 m. appear to be its upper limit of distribution. These altitudes are clearly roughly proportional to the heights of the mountain masses in the different countries.

(7) *M. ovata* is the other important member of the Central European subgroup. Like *M. perennis* it is also an unbranched perennial species which propagates itself chiefly by vegetative reproduction. It agrees in many essential respects with *M. perennis*, the chief point of distinction being based on the characters of its leaves, which differ from those of *M. perennis* in that they are sessile or subsessile, orbicular or ovate (cf. the “Clavis specierum” of Pax, p. 42)—features which after all are not so very important from the taxonomic point of view, especially in judging specific rank.

*M. ovata* occurs in many parts of Central Europe, but it attains its greatest vigour and importance in the south-eastern region. Like *M. perennis*, however, it may be frequent to abundant in its distribution or may be entirely absent over large stretches of country. This is especially the case in the central alpine valleys and in western Germany, also in many parts of Switzerland and Tirol. As compared with *M. perennis*, this species is thus on the whole rather localised in its distribution.

*M. ovata* grows in clumps under the shade of woodland trees or bushes, on loamy and clayey soil, on sandy and stony ground and also in calcareous habitats. It occurs both in the plains and on the mountains, its altitudinal range of distribution hardly ever exceeding 1800 m.

Like *M. perennis*, it is often found growing in association with a number of other herbaceous species such as *Allium ursinum*, *Leucojum vernalis*, *Gagea lutea*, *G. spathacea*, *Corydalis fabacea*, *Anemone ranunculoides*, *Euphorbia dulcis* and others.

#### (ii) *Eastern Asiatic group*

From the preceding account it will be abundantly clear that though a large majority of the aggregates are confined to Europe and the adjoining Mediterranean region, including the northern parts of Africa, yet there is a small group which occurs in the Far East apparently detached from this main body.

Until the year 1914 there was only one species known, *Mercurialis leiocarpa* Sieb. et Zucc., which was considered to be the sole representative of the genus in this part of the world (cf. Pax, 1914), but another new species called *M. transmorrisonensis*, which is supposed to be a native of the island of Formosa, was afterwards added to this group by Hayata.

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(8) *M. leiocarpa* Sieb. et Zucc. bears a very close resemblance in its morphological characters to *M. perennis* L. Like the latter, it is an unbranched perennial herb which propagates itself extensively by means of rhizomes. Like *M. perennis* again, although normally a dioecious plant, it sometimes produces monoecious forms. According to Pax (1914) the chief distinguishing feature which separates these two species is that the ovary and capsule of *M. perennis* are pubescent while those of *M. leiocarpa* are glabrous. In the light of my own investigations, however, it is doubtful if we are justified in calling *M. leiocarpa* Sieb. et Zucc. a separate species (cf. p. 50 *et seq.*).

Whatever the origin and the systematic rank of this species may be, it is certainly of interest to note in this connection that it is fairly widely distributed in the Far East, where it extends from Japan in the north to Siam in the south. It is said to be absent from the northern part of Japan—approximately above lat. 38° N. In the southern parts of Japan it grows abundantly, often in dense patches, so that it may sometimes form the major portion of the ground vegetation of several types of deciduous woods. It also occurs in Formosa and in a number of smaller islands off the eastern coast of China. It is of particular interest to note in this connection that on the mainland of China itself, *M. leiocarpa* has so far been recorded only from the province of Yunnan, where it is reported to occur over large areas. Further south, *M. leiocarpa* extends well into Siam, where it is supposed to have reached its southern limit of distribution at the present day. In many parts of Siam it occurs in dense patches as the principal element of the ground vegetation of several types of deciduous woodlands. Both in China and in Siam it grows in the plains as well as on the mountains. Altitudinally it may even attain a height of about 10,000 ft., as is recorded by George Forrest and other botanists.

It may be mentioned here that a prostrate trailing form of *M. leiocarpa* has been recorded from Siam. A similar trailing form of *M. perennis* has been collected by the author from certain localities in Britain.

(9) *M. transmorrisonensis*. This is a new species described by Hayata, according to whom it is restricted to the island of Formosa (*vide Ic. Fl. Formosa*, v, 199 (1915)). I am unable to say anything about this particular plant, as no material was available for examination in the various herbaria that I visited in England and on the Continent.

### DISCONTINUOUS DISTRIBUTION OF THE GENUS

When one looks at the map of the world (p. 49) showing the distribution of all the known species of *Mercurialis* in nature, the discontinuous character of the distribution of the genus at once becomes apparent. The two Far Eastern species of *Mercurialis*, viz. *M. leiocarpa* and *M. transmorrisonensis*, are separated from the Western species by a wide interval. As far as our present knowledge goes, this intervening region is entirely devoid of any representative of the genus *Mercurialis*. But when the taxonomic characters

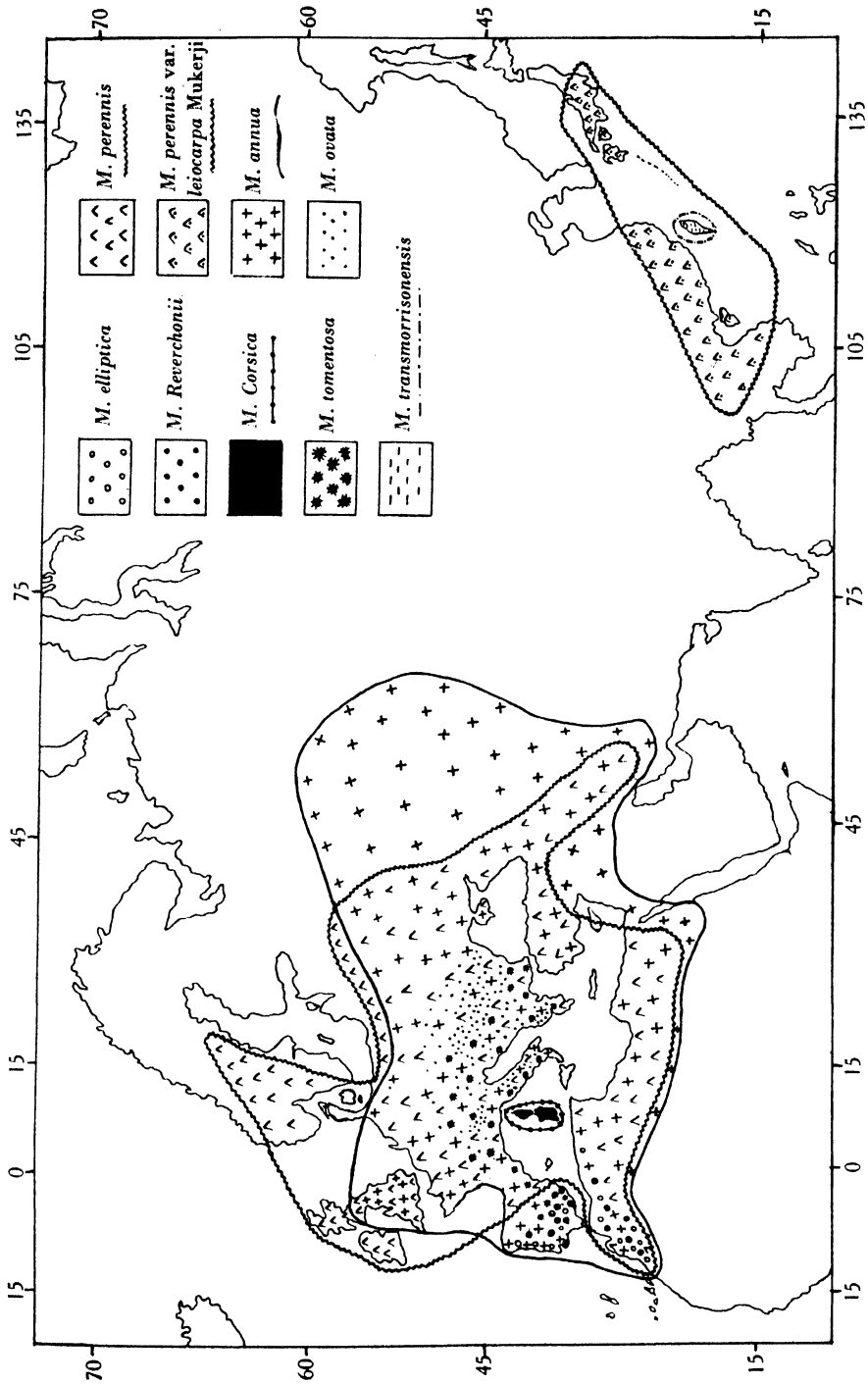
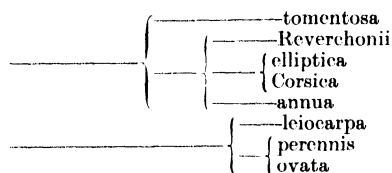


FIG. 1. Sketch map showing the geographical distribution of the genus *Mercurialis*. The distributions of *M. annua*, *M. Corsica*, *M. perennis*, *M. perennis* var. *leiocarpa* and *M. transmarionensis* are shown in outline as well as by symbols.



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of the species that lie immediately on either side of this broad belt are critically examined and compared, it is soon realised that *M. leiocarpa* of the Far East has a closer affinity with the members of the Central European subgroup, viz. *M. ovata* and *M. perennis*, especially with the latter, which extends to the border of the broad belt mentioned above, than with those of the Mediterranean subgroup, viz. *M. elliptica*, *M. Reverchonii*, *M. annua*, *M. tomentosa* and *M. Corsica*. Pax in *Das Pflanzenreich* (1914) diagrammatically represents the affinities of the species thus:



In fact the general similarity between the morphological and biological characters of *M. leiocarpa* and *M. perennis* is so close that one might at first sight easily mistake the one species for the other, the chief point of distinction being the glabrous ovary and capsule of the former, while those of the latter are hairy. This raises the question of the specific rank of *M. leiocarpa* Sieb. et Zucc. From a close study of the morphology, biology and ecology of *M. perennis*, both in nature (in Britain and various countries of Central Europe) and under cultivation, I have come to the conclusion that this species is very plastic and variable in its characters, including the hairiness of the ovary and capsule, when the plant is cultivated under varying conditions of illumination and also under different edaphic conditions. Again, according to the researches of Krasan (1865) *M. ovata* is stated to change into *M. perennis* after about six months of cultivation. This remarkable observation, coupled with the resemblance in the aggregate of characters between the two species and also the great variability and plasticity of *M. perennis*, tends to suggest that *M. leiocarpa* may not deserve definite specific rank, but should rather be considered as an eastern form of *M. perennis* L.

With the object of settling this point, I have carried out an extensive examination of the herbarium material of all the species of *Mercurialis* in some of the principal herbaria of Europe. When examining the herbarium sheets of *M. leiocarpa* at Kew, I came across a specimen (No. 4598) collected by George Forrest from western Yunnan (China) in 1906. It bears the following description: "4598. *Mercurialis leiocarpa* Sieb. et Zucc. Plant of 6 to 12 inches. Flowers green. Moist shady situations in side valleys on the eastern flank of the Tali Range. Lat. 25° 40' N., altitude 8000 to 10,000 ft. June-July 1906, W. Yunnan, China. This species is not known from the Himalayas but was recently found in Northern Siam by Dr Hosseus."

Dr W. B. Turrill of the Kew Herbarium and I came to the conclusion that *this particular specimen was in every respect indistinguishable from M. perennis*

*L.*, even the ovaries and young capsules being markedly hairy. Further support was obtained when we examined the Edinburgh Herbarium. Here again the Edinburgh duplicate of the Kew No. 4598 was indistinguishable from *M. perennis* L. Moreover, a monoecious form marked *M. leiocarpa* Sieb. et Zucc. was also observed among these sheets. This would accord with the recorded cases of monoecism in *M. perennis* L. noted in Britain and elsewhere.

Thus there seems no alternative but to consider that *M. perennis* L. also occurs in the eastern Asiatic region, and there is therefore no reason for considering *M. leiocarpa* Sieb. et Zucc. as more than a variety of *M. perennis* L.

In the light of these facts, the apparent absence of *M. perennis* from the Central Asiatic region may perhaps be attributed to our relative lack of knowledge of the floristics and ecology of this region. There does not appear to be any valid reason why *M. perennis* L. should not occur in this Central Asiatic region though no records of its existence are available, especially when we remember that some of its principal associates in the west, such as *Asperula odorata*, *Arum maculatum*, etc., do extend right up to the Pacific coast of Siberia and China and have been actually recorded in localities from which *Mercurialis perennis* is supposed to be absent.

It is of interest to note that the herbarium specimens of *M. leiocarpa* both at Kew and in Edinburgh may be placed under three groups as follows:

(1) *Plants which bear distinctly hairy ovaries and capsules*—e.g. specimen No. 4598 of Kew. Such types, so far as is known at present, only occur in the western parts of the area of its distribution.

(2) *Plants with sparsely hairy ovaries and capsules*. These are intermediate forms occurring in central Yunnan, Korea, etc. Specimen No. 10,477 of the Edinburgh Herbarium (collected by A. Henry in Yunnan-Feng; 6000–8000 ft. in forest on Chin Lin Peak) is a good example of this type.

(3) *Plants with definitely glabrous ovaries and capsules* occur chiefly in the eastern parts of its area of distribution. For example, all the specimens from Japan have perfectly glabrous ovaries and capsules.

Hence we notice that in the area of distribution of *M. leiocarpa* itself the hairy character of the ovaries and capsules borne on the plants that grow in the western parts gradually passes into the completely glabrous condition of those that occur in the east.

Taking into account, therefore, all the above considerations I venture to suggest that *M. leiocarpa* Sieb. et Zucc. is only a variety of *M. perennis* L., and with this conclusion some of the specialists of the Kew Herbarium agree. I therefore propose the following amended citation of these forms:

*M. perennis* L. *Sp. Pl.* 1037 (1753) var. *leiocarpa* (Sieb. et Zucc.) Mukerji, nov.comb. *Syn. M. leiocarpa* Sieb. et Zucc., *Fl. Jap. Fam. Nat.* 1, 37 (1843).

So far as our present meagre knowledge goes, the genus shows a well-marked discontinuity in its distribution, for out of a total of eight species,

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according to our present scheme, six are confined to Europe and the adjoining Mediterranean region, while one species, *M. transmorrisonensis*, occurs exclusively in Formosa in the Far East. The eighth species—*M. perennis*—has the widest distribution of all. It extends over the greater part of Europe, occurs in the Mediterranean region and in Asia Minor, and extends from Caucasus to Persia in the east. Then, after an absence over a wide area in central and western China and Siberia, it reappears once again in the Far East in the Chinese province of Yunnan. Here one of its principal varieties, viz. *M. perennis* var. *leiocarpa* Mukerji, occupies a dominant position as regards distribution and growth. Thus it is almost certain that the genus is of greater antiquity in the west than in the Far East, the majority of the species having their centres of development in Europe.

The most obvious interpretation of these facts is to suppose that the migration of the genus has taken place from west to east, and that *M. perennis* was the species which actually migrated across the continents. Hence there is every reason to believe that *M. perennis* must have grown in those regions whence we have no available records of its existence at the present time; and from which, therefore, it is supposed to be absent.

It is quite possible that the supposed absence of *M. perennis* or any other species or varieties of *Mercurialis* from Central Asia is merely due to our inadequate knowledge of the flora of that part of the world. This view is strengthened by the fact that the people who were responsible in the past for collecting plant specimens from the interior and remote parts of China and Central Asia in general, were mostly men who were interested in plants with showy, conspicuous flowers and fruits, mainly for horticultural purposes. It is therefore natural to presume that such plants as *M. perennis* and its allied species with tiny inconspicuous greenish yellow flowers may have been completely neglected even if present in their collecting grounds. I think it very probable that some day *M. perennis* or some other representative of the genus will be found in this Central Asiatic region where it is supposed to be absent. According to this view the discontinuous distribution of the genus *Mercurialis* is only apparent and not real.

Another consideration must not be neglected. The genus *Mercurialis* possesses two wide-ranging species, *M. perennis* and *M. annua*. All the other species are included in the area of distribution of one of these two wide-ranging forms. Hence the possibility must not be lost sight of that the more restricted types represent specialised forms within the wide-ranging ones as suggested by Guppy (1907) in his so-called "Differentiation Hypothesis".

## PART II. THE SEED AND DEVELOPMENT

## THE SEED

The seeds of *M. perennis* are usually round, ovoid or subglobular, being pointed or crested at the apex. On an average they measure 3 mm. in diameter and weigh approximately 0.0078 gm. They are covered on the outside with a thick coating of rather tough consistency. This outer coat bears finely reticulated markings and has a somewhat shiny surface of bluish grey tint. The seed does not become sticky on moistening and appears to be in no way adapted for animal dispersal except that at its base near the point of attachment of the hilum there is developed a whitish caruncle which partially envelopes the seed and which may be concerned in its dispersal by ants (see p. 77).

In the partially ripe condition the pearly white kernel practically fills up the entire space inside the seed-coat; but as the seed dries in the process of ripening, the endosperm shrinks from the testa and begins to shrivel up into a tiny albuminous mass, ultimately leaving a cavity all round except at the point of attachment to the testa.

On breaking open the seed-coat and dissecting the endosperm under a binocular microscope, one can with a little practice isolate the minute embryo from the rest of the albuminous mass in which it is embedded. The embryo possesses two fairly well-developed, foliaceous cotyledons which lie flat against each other. They enclose between them a more or less rectangular block of tissue—the *plumular bud*—which surmounts a rod-shaped structure—the *hypocotyl and radicle*.

The weight of the seeds also varies to an appreciable extent. The same number of seeds (500) collected from several localities gave different weights. This will be evident from Table I.

Table I. *Weights of batches of 500 seeds from different localities.*

Locality	Date of collection	Weight of batch, gm.
Woldingham	June 1926	3.54
Woldingham	..	4.21
Orpington	..	3.91
Boxhill	..	3.40
Purley Beeches	June 1927	4.17
Staplehurst	..	4.52
Coulsdon	..	3.72

It was also found that in a number of cases the seeds collected from the earlier crops, i.e. in the early part of the flowering season, were heavier in weight and larger in size than those collected later in summer. The data at present available do not, however, enable us to say whether this is of general application.

## SEED OUTPUT IN BRITAIN

According to Gillot (1925), the harvest of seeds of *M. perennis* in France varies considerably from year to year. In some years a very large quantity of seed may be produced, while in others the crop may be very poor indeed. I find that this is the case in England also. Further, the harvest of seeds gathered in one and the same season from different widely separated localities in Britain varies to a remarkable extent. For instance, the total number of seeds collected in June 1926 from numerous batches of 100 female shoots of *M. perennis* growing on a chalky hillside near Boxhill amounted to 520 per hundred shoots or an average of 5.2 seeds per shoot, while 100 female shoots from Woldingham gave as high a figure as 1565. The two collections were made during the same week. The highest yield obtained by me was in June 1927 from Purley Beeches, where each female shoot on an average produced thirty seeds. The highest record for an individual shoot so far observed is forty-two seeds. This was obtained from Staplehurst in Kent in June 1926, from a very vigorous and robust plant which attained the unusual height of 62 cm. An adult plant of *M. perennis* may bear from five to forty shoots, so that the seed output per plant hardly ever exceeds 1680 and averages about 300. This is a very low seed output indeed as compared with that of many other species. For example, the number of seeds produced on a single plant of *Verbascum thapsus* of average size ranges from 27,000 to 700,000, and that of *Digitalis purpurea* from 59,000 to 490,000 (cf. Salisbury, 1924).

On the other hand, in certain localities cases of extreme sterility may be met with. In June 1926 I came across a fairly big clump of female plants which were growing under the dense shade of *Quercetum roboris* near Staplehurst. The place was very humid. The soil was heavy clay, the natural water content of which was 96.2 per cent. during the spring months. The light intensity on the ground in the region of the *Mercurialis* patch was 1.5 per cent in the "shade phase". There was an entire lack of flower production, although the plants were unusually vigorous and healthy. Here was a case where an entire patch of female plants had used all their available resources in the production of very vigorous and healthy vegetative organs at the expense of reproductive parts, probably under the influence of shade conditions inadequate to flower formation but sufficient for vigorous vegetative growth, to which the high humidity also contributed.

Apart from these conditions of extreme shade and humidity the following factors are important in influencing the production of seed. If the plants are exposed to strong winds and rain at the time most favourable for pollination there is loss of a large proportion of the pollen grains, and a large number of the female flowers shrivel up owing to lack of fertilisation. In such cases the chances of production of viable seeds are naturally greatly diminished. This was actually observed to have taken place in a number of localities visited;

the most striking example was in a yew wood on the western slope of Boxhill. Although male and female plants were growing side by side strong wind and rain had prevented pollination. The result was that all the female flowers borne on the lowest four or five axillary spikes had withered and completely shrivelled up.

On the other hand, wind pollination may be greatly augmented by animal agencies such as bees, flies, ants and night-flying moths and butterflies. This was first observed by me on some female clumps of *M. perennis* at Staplehurst, where insects of the kinds mentioned above were taking a substantial part in pollination; and I have seen the same thing in quite a number of other places. This supplementary insect pollination would naturally result in a far greater proportion of female flowers being pollinated, and consequently in an increased amount of seed production.

A certain amount of sunshine accompanied by relatively dry conditions is necessary for the proper ripening of seeds in nature. Too weak light with continued wet weather at the critical period when the seeds should ripen has been observed not only to cause delay in the ripening of seeds, but to prolong their shedding and ejection from the fruit case. Prolongation of the period of ripening and ejection of seeds till the autumn rains set in and the temperature falls are factors very detrimental to the harvest of seeds, and may result in early death of the entire crop of fruits or in the shedding of unripe and non-viable seeds. Ground bearing a dense crop of *M. perennis* may often be seen in the summer to be strewn with prematurely shed fruits and unripe seeds (in some cases partly devoured), and this is often the result of inclement weather conditions such as prolonged cloudiness, strong winds, heavy rain and low temperature.

#### GERMINATION OF SEEDS IN NATURE

The seed output of *M. perennis* in Britain is, as we have seen, not large compared with many other woodland species, varying from three to thirty per shoot with an extreme record of forty-two. Further, the percentage of germination is decidedly low in relation to the actual production of seeds. Till recently, indeed, it was believed by many botanists in England that the germination of seeds of *M. perennis* did not take place at all in nature, and that this plant exclusively propagated itself vegetatively by copious production of rhizomes. The seedlings certainly appear to be rather rare in nature. After a prolonged search in the spring, a fresh crop of young seedlings of the current year may sometimes ultimately be discovered, each still provided with the two foliaceous cotyledons.

In March 1926 I was successful for the first time in collecting a few seedlings of this species, in various stages of development, from a beech-yew wood not far from Boxhill. Since then, I have been able to collect seedlings from a number of other wild stations including Woldingham, Orpington,

Chiselhurst, Staplehurst, Coulsdon, Purley, Westerham, Reading, etc. This does not mean that they are of common occurrence, for patient and prolonged search for seedlings in a large number of widely separated localities has very often given negative results. Seedlings of *M. perennis* are undoubtedly rare in nature. Any number of tiny plants looking just like seedlings and possessing two or three pairs of small leaves may be encountered. But on closer examination most of these will be found to be aerial shoots given off from the axils of scale leaves borne on pre-existing rhizomes.

#### FACTORS DETERMINING SEEDLING FREQUENCY

The rare occurrence of seedlings in nature is brought about by a number of adverse factors of which the following may be mentioned.

(1) *Defective (malformed) seeds.* Malformation of seeds is one of the most important causes of the very low percentage of germination in nature. A careful examination of several thousands of seeds of *M. perennis* collected from different localities in Britain brought to light the fact that enormous quantities were absolutely unfit for germination. Deformity or malformation of seeds is a common experience in dealing with any quantity of seeds collected from wild stations. Gillot (1925) also emphasises this fact in connection with his French collection. I agree with him when he says that as high a proportion as about 75 per cent. of seeds are defective and non-viable. A majority of such defective seeds are found on dissection either to have abortive embryos or none at all. If such defective seeds are allowed to soak in warm water they readily swell and show signs of germination. But when actually sown in pans or in wooden boxes containing good garden soil, natural woodland soil or leaf-mould, and kept under conditions best suited for germination, no trace of any elongation of either the radicle or the plumule can be detected. They remain in the swollen condition for some time, but invariably every one of them perishes in the end, some becoming densely covered with a felt of fungal hyphae.

(2) *Seeds destroyed by birds and other animals.* One often comes across a large number of seeds of *M. perennis* strewn on the floor of a beech- or oakwood, which when examined with a lens, are soon found to be merely remains of the original seeds in the form of punctured shells with no kernel inside. The outer shell has been ruptured and the enclosed albuminous endosperm eagerly sought and devoured by birds and other animals. On several occasions I have watched at close quarters the mother pheasants accompanied by their young feeding voraciously on these seeds, eating the kernels and leaving the shells behind. Field-mice probably also claim a share in the destruction of these seeds. In June 1926 several hundred seeds were sown in pans in the laboratory and kept in a warm moist place. After a week it was discovered that mice had suddenly attacked the seeds one night and had devoured the kernels of each and every one of them. Although I have no direct evidence of field-mice behaving similarly towards the seeds of *M. perennis* in nature, yet it is clearly

quite probable that they do so, having regard to their known behaviour towards acorns and beech-nuts.

(3) *Decay of seeds and seedlings from fungal attack.* It has already been pointed out that seeds of *M. perennis* require a certain resting period before they can germinate. During this time, as they lie on the ground, they are fully exposed to the danger of fungal infection. Sometimes apparently healthy and well-developed seeds are infected with fungi in this way and ultimately reduced to a black powdery mass. Such fungus-stricken seeds are often met with in woodlands early in spring. Even when seeds escape death from fungal attacks and give rise to young seedlings which become firmly established in the ground, the danger of infection is not over, for the seedlings themselves occasionally fall victims to the various types of pathogenic fungi which are always present in the soils of woodlands, as has been demonstrated by Brierley, Waksman and other workers (cf. Russell, 1927).

(4) *Germination hampered by unfavourable conditions.* Seedlings were found to be definitely absent from certain localities, although the female plants growing in such localities apparently set quite a large amount of ripe seeds. Comparison of analyses of soil samples from such localities where no seedlings could be found with samples collected from areas where dozens of seedlings occurred, suggested that certain soil factors might have a deleterious effect on the germination of seeds in nature.

It was found, for instance, that high hydrogen-ion concentration ( $pH$  4.5), coupled with low water content (below 15 per cent.) and a very low soil temperature (about  $34^{\circ}$  F.), were some of the factors which might have been responsible for the non-germination of seeds and consequent lack of seedlings. Then again, strong insolation (above 60 per cent.), excessive water content of the soil (above 60 per cent.), and a highly alkaline reaction of the soil (above  $pH$  7.8), appear to have a markedly deleterious effect on germination of the seeds of *M. perennis*. Soil data from a large number of localities where seedlings were definitely absent justify these suggestions. Seeds collected from some of these places where seedlings were definitely absent did actually germinate, when placed under suitable conditions, so that the absence of seedlings could not be attributed to non-viability of the seeds.

(5) *Immature seeds.* Experiments were carried out in the laboratory to find out whether partially ripe seeds would germinate or not. More than a thousand seeds of this kind were sown in batches of fifty and a hundred each at different times of the year under the most suitable conditions for germination. In no case did any seed germinate. In nature, however, the shedding of partially ripe seeds and immature fruits is a common feature. It is therefore naturally an important factor responsible for the low percentage of seedlings in nature.

(6) *Burial of seeds.* A certain number of seeds get buried under debris and earth brought to the surface in woodland soils by such burrowing animals as



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rabbits, moles and earthworms. Again, some seeds find their way accidentally or otherwise into holes of earthworms and burrows of other animals. Such seeds stand extremely poor chances of germination, for actual experiments on deep sowing with seeds of *M. perennis* showed that no germination takes place under such conditions.

Thus it will be evident that the rare occurrence of seedlings of *M. perennis* in wild stations in Britain is brought about by a variety of factors—climatic, edaphic and biotic—which work severally or jointly according to the situation in which the plants happen to grow.

### EXPERIMENTS ON GERMINATION

Over two thousand seeds of *M. perennis* were sown from time to time in batches of 50, 100 and 200, in pans and in wooden boxes containing various kinds of soils, such as natural woodland soils, sterilised and unsterilised garden soils, peat, loam, sand, clay and leaf-mould. These pans and boxes were kept under favourable conditions of warmth, moisture and atmospheric humidity, in suitable places, some in bright light and others in the dark, any large fluctuations of temperature being always avoided.

The progress of these experiments was closely followed and recorded from time to time. The results obtained tend to show that the percentage of germination is in all probability lower in England than it is in France as recorded by Gillot (1925), who has succeeded in getting 15–25 per cent. of germination. In my experiments the highest figure ever obtained from a batch was 10 per cent., and the average germination of the whole collection was 5 per cent. This will be evident from Table II.

Table II.

Locality	Date of collection of seeds	Date of sowing	No. of seeds sown	Date of germination	Total number germinated	Germination %
Woldingham	June 1926	Sept. 1926	200	Jan. 1st–10th, 1927	10	5
Orpington	May 1926	June 1926	200	Sept. 5th–20th, 1926	9	4.5
Boxhill	June 1926	July 1926	100	Oct. 10th	1	1
Staplehurst	June 1926	Mar. 1927	200	May 7th–18th, 1927	20	10
Coulsdon	June 1926	Oct. 1926	50	Jan. 1st–5th, 1927	2	4
Purley Beeches	May 1926	Aug. 1926	200	Feb. 2nd–12th, 1927	16	8
Sevenoaks	July 1926	Sept. 1926	100	May 3rd–10th, 1927	3	3
Watford	June 1926	Aug. 1926	200	April 10th–20th, 1927	20	10

Owing to the low percentage of germination, it was considered advisable to try some artificial devices for stimulating the seeds to germinate, such as are sometimes used in cases of difficult and delayed germination, e.g. in seeds of *Hevea brasiliensis*, *Epilobium roseum*, red clover, etc.

Numerous cases are known where hard seed-coats inhibit germination, which takes place as soon as these are removed. The seed-coat may act by preventing the absorption of water or the intake of oxygen or by offering severe mechanical restraint. In *Alisma plantago*, for instance, Crocker and

Davis (1914) found that the seed absorbs water readily, with the result that the embryo swells up and presses against the restraining seed-coat with a force of about 100 atmospheres, but even then it cannot rupture the testa and so is unable to germinate.

Then again, it has been recorded that seeds of broom may lie for months together on moist filter paper without undergoing any change, but when a slight scratch is made on the testa the seed readily absorbs water and swells up, germination following in a day or so. This behaviour is of practical importance and has been taken advantage of in the germination of such commercially important seeds as those of red clover and spinach, which are often artificially abraded to secure more rapid and complete germination. In other cases exposure to frost seems to be necessary.

De Vries (1915) found that the germination of *Oenothera* seeds was greatly improved by forcing water into them under pressure. Lehmann (1911) found that the seeds of *Epilobium roseum*, and a few other plants which normally germinate under conditions of bright illumination, can be made to germinate in the dark if exposed to a sudden rise of temperature. Similar methods were therefore tried with the seeds of *Mercurialis perennis* to see if a higher percentage of germination could be obtained. 200 seeds were kept overnight fully exposed to frost on February 10th, 1927. Next morning they were sown in a pan containing natural woodland soil brought from a locality near Orpington where seedlings were growing in a healthy condition. For a time the seeds retained their vitality, but eventually they all perished without germinating. It was therefore apparent that exposure to frost before germination did not serve any useful purpose.

Again, a batch of 200 seeds was allowed to soak in tepid water for nearly 2 hours, with a view to softening their hard outer coats. This treatment also did not appreciably improve matters, as only four seeds out of 200 germinated.

Finally, germination of partially ripe seeds was attempted. For this purpose, a thousand seeds were collected from different localities in a partially ripe condition, while still attached to the parent plant body. They were brought to the laboratory and 600 of them were sown immediately in three batches of 200 each on three different kinds of soils, viz. leaf-mould, good garden soil and finely powdered clayey-loam from Woldingham. Although they rapidly swelled up and showed signs of germination, yet not one of them in either of the three sets ever gave rise to a seedling. The experiment was started on May 16th, 1926, and by June 25th following practically the whole of the 600 seeds had perished.

As a result of these experiments it may be said first of all that healthy, fully formed and ripe seeds alone stand any chance of germination, while those in any way short of maturity may be considered as worthless.

Secondly, a period of rest seems to be indispensable before germination can start. In this connection it may be pointed out that seeds collected in

May 1926 and kept in airtight bottles in darkness gave the best results when sown in February 1927. It was from them that the maximum percentage of germination, viz. 10 per cent., was obtained.

Thirdly, seeds freshly gathered and sown immediately never germinate. That seeds sown in the same season in which they ripen do not germinate has been repeatedly brought to my notice during the course of my field work extending over a large area of the south of England. For instance, the earliest stages in the germination of seeds in nature were invariably obtained in the period between February and April, i.e. at a time when there could be no possible chance of the shedding of ripe seeds of the current year, as the flowers on the female plants themselves were all very young in localities where seedlings up to 5 cm. in height were found growing. These seedlings were undoubtedly a result of the germination of the previous year's stock of seeds which had lain on the ground for 9 months or so and thus had passed through a definite period of rest before they had germinated.

#### MODE OF GERMINATION

The germination of the seeds of *M. perennis* either takes place in autumn or at the approach of spring immediately after the winter rest. Under suitable conditions of warmth, atmospheric humidity and soil moisture, the first stage in germination is marked by the swelling of the seed, which results in a partial rupture or splitting of the seed-coat. A few days later the radicle pushes its way through the micropyle and bending downwards penetrates into the soil. As growth advances this radicle develops into the primary root system of the plant. It is followed by an upward elongation of the plumular bud which, having forced its way from its position of confinement between the two rounded cotyledons, now grows upwards and surmounts the hypocotyledonary axis. In the course of further development this grows into the unbranched aerial shoot of the plant. The cotyledons are the last to emerge from the seed-coat, which is sometimes seen still attached to one of them. The details of germination have been described by Gillot (1925), with whom I entirely concur, and hence they do not require repetition here.

The position of the cotyledons in relation to the soil surface during germination varies considerably. In some cases they are epigeal, emerging above ground, in others they remain just below the surface or on a level with it, while in others again they remain buried, sometimes 4 cm. or so below the soil surface. In the majority of cases, however, the germination is distinctly *hypogeal*; and then the cotyledons have a pale yellow colour. In those cases where the cotyledons come above ground, they develop chlorophyll and function as assimilatory organs for some time.

DIFFERENCES BETWEEN SEEDLING OF *MERCURIALIS PERENNIS* AND *M. ANNUA*

I have sometimes been asked how I am able to say definitely that the seedlings encountered in nature are those of *M. perennis* and not of *M. annua*, which also occurs widely in Britain though normally in totally different habitats.

Four prominent features distinguish the seedlings of the one species from the other:

- (1) In comparable specimens of seedlings of approximately the same age, the hypocotyledonary axis of *M. annua* is bigger than that of *M. perennis*.
- (2) The cotyledons of *M. annua* are generally epigeal, while those of *M. perennis* are generally hypogeal. The elongation of the hypocotyl of *M. annua* is partly responsible for this. The cotyledons of *M. annua* have longer stalks than those of *M. perennis*.
- (3) The lowermost pairs of foliage leaves in *M. annua* are decidedly bigger than those of *M. perennis*, whose foliar organs below the middle of the stem are generally rudimentary and minute.
- (4) The branching habit of the shoot of *M. annua* becomes quite apparent from the very beginning, when branch buds appear in the axil of the first pair of leaves. No such buds are to be seen in the axils of the first pair of leaves in a seedling of *M. perennis*, whose shoot remains unbranched.

## DEVELOPMENT TO ADULT

It is generally in the month of February that the first pair of foliage leaves begins to appear on the seedlings which had germinated in the autumn. At this stage the shoot attains a height of 10–12 cm., and the main root goes down to a depth of about 8–10 cm.

In their earlier stages of emergence from the ground the seedlings are composed of the following parts:

- (1) *Stem*, 2–4 cm. high and terminated by a bud which is surrounded by two small leaves.
- (2) *Axis of the hypocotyl*, which is thicker in diameter than the radicle and from which one or two lateral rootlets are given off at this stage.
- (3) *Two cotyledons*, which are fully expanded. They sometimes persist for several months.
- (4) *Primary root*, with one or two secondary rootlets.

The terminal bud develops and the aerial shoot bears four or five pairs of leaves at the end of 2–3 months. During this time one or two adventitious roots are given off either from the summit of the hypocotyl or from the cotyledonary node itself, sometimes even arising directly from the axil of the cotyledons. These adventitious roots often go down deep into the soil, attaining a depth of 15–20 cm. and bear very few secondary rootlets. They are considerably thicker in diameter than the primary roots.

During the summer the aerial shoot attains its full development and there is also considerable increase in the root system. By this time the cotyledons are shed and tiny buds begin to appear in their axils. These buds generally manifest themselves at the time of appearance of the second pair of leaves. Each cotyledonary bud soon becomes the centre of origin and development of a system of ramification—the complex network of rhizomes. Each axillary bud bears two minute scales enclosing the terminal portion of the bud which later develops into a branch of the first order. When the terminal bud elongates new lateral buds appear in the axils of its two basal scales. Each of these lateral buds also bears two scales of limited development surrounding a terminal bud of a branch of the second order. This latter branch (of the second order) elongates in its turn and very early shows at its base two axillary buds which in their turn will give rise to branches of the third order. If all these branches were to develop equally there would result, in a given plant, two branches of the first order, four of the second and eight of the third.

This system of ramification which arises from the region of the cotyledonary node develops more or less according to circumstances. For instance, when the cotyledons are carried above the soil, which is exceptional, the buds situated in their axils develop into leafy branches as soon as the plant possesses two or three pairs of leaves. But this sort of branching above ground is very exceptional indeed. Normally the cotyledonary node remains underground and the branches which belong to the three categories mentioned develop into a subterranean rhizome system. In nearly all cases the developing seedling possesses subterranean branches of the first and second order, but no matter to what category the branch may belong, each possesses two buds at its base. Of these buds some develop into rhizomes while others remain dormant.

This subterranean activity in the formation of rhizomes generally takes place towards the end of spring and early in summer, when all further growth of the subaerial parts practically comes to an end. The rhizomes then assume active growth, spreading horizontally at varying depths in different directions. This kind of underground growth is very active throughout the summer, but it slows down considerably as the winter approaches.

The rhizomes are whitish in colour and measure 2–3 mm. in diameter; their length, after they have attained their complete development, varies from 5 to 50 cm., so that at the end of the first growing season a single plant may extend over an area of about 75–7500 sq. cm. At this stage a fully formed rhizome possesses two to four nodes, each of which bears a pair of minute scale leaves. The internodes show a good deal of variation in length. It is also not unusual to find rhizomes that are covered all over with a dense coating of unicellular hairs (analogous to root hairs), especially in soils that have a high organic content.

The tip of each rhizome bears a well-differentiated terminal bud which at the commencement of the growing season, i.e. at the end of January or be-

gining of February, assumes an erect position and reaches the surface of the soil. As growth advances the terminal bud is protected by the development of a pair of foliage leaves which enclose it completely. The apical part of the rhizome now becomes bent in the form of a loop, and it is generally in this condition that the tip emerges from the ground. The terminal bud straightens out and once again assumes an erect position after its emergence. It then becomes an aerial shoot of the plant.

The annual growth is henceforward manifested by the formation of the following parts:

(1) *An underground perennial part*, which consists of rhizomes, roots and root stocks, and

(2) *An aerial part*, represented by the aerial shoots which die down to the ground every winter, and are formed afresh at the beginning of each growing season.

At this stage the primary root system becomes sufficiently extensive to be able to cope with the demands of the growing aerial shoots, but on the resumption of vegetative activity during the next spring new roots are developed adventitiously from the nodes of the rhizomes. At the same time, the buds borne in the axils of scale leaves on these nodes begin to produce new sets of branches which constitute a fresh network of rhizomes; these latter in their turn behave exactly in the manner described above, and their ultimate vegetative activity results in the formation of new crops of rhizomes, aerial shoots and roots.

Thus plants newly produced in nature by the germination of seeds confine their activities to vegetative growth, establishing themselves in the ground and spreading in different directions by means of underground rhizomes. In most cases the reproductive stage, viz. the production of flowers and fruits, does not normally begin before the third year of growth. Once the flowering has begun, new plants come into existence both by the germination of seeds and by the detachment of branches through the decay of the older parts of rhizomes.

### PART III. BIOLOGY OF THE ADULT PLANT

#### THE ROOT SYSTEM

Two kinds of roots are borne by *M. perennis*:

(1) *The "seminal" roots*, i.e. those that belong initially to the embryo, and others which develop later, either from the hypocotyl or the cotyledonary node, and

(2) *Adventitious roots*, which are given off from the stem of the adult plant.

As previously mentioned, the embryo possesses three to five roots, viz. a primary root and one or two pairs of lateral rootlets which originate either

from the hypocotyl or the cotyledonary node. They may arise even from the axils of the cotyledons. The primary root system may last for 4 or 5 years, during which period it produces a large number of lateral rootlets. The adventitious roots usually remain unbranched or may branch rather sparingly.

The root systems of those newly formed plants which arise by vegetative multiplication from the nodes of the rhizomes produced by the original seedlings are always formed adventitiously. Two types of these roots are distinguishable, branched and unbranched. In the young condition both types are whitish in colour, but as they grow older they turn yellowish brown due to suberisation. The unbranched roots generally become thicker and more suberised than the branched ones. They penetrate more or less vertically into the soil and appear to function mainly as fixing organs. The branched type with its ramifying network of fine laterals, its further increase of surface by a felt-like coating of root hairs and its mycorrhizal character, is mainly concerned with the absorption of water and nutrient salts from the soil. The roots of *M. perennis* are almost invariably mycorrhizal. The branched type of roots, particularly, usually reveal the presence of fungal hyphae, while the unbranched ones may or may not be infected.

Bernard and others have suggested that the mycorrhiza plays an important part in bringing about the formation of swollen underground structures, e.g. root stocks, tubers, or corms, found in so many kinds of plants. Magrou (1921) believes that in *M. perennis* the presence of mycorrhiza is responsible for the development of the perennial underground organs, viz. the rhizomes. He correlates the absence of any similar perennating organs in *M. annua* with the non-occurrence of mycorrhiza in that species.

The roots of *M. perennis* bear a large number of root hairs which arise a short distance behind the apex. As the root system penetrates more deeply new root hairs are produced and the older ones shrivel up and finally drop off. An interesting feature is the intercalation of new root hairs between the older ones (Fig. 2): some of these root hairs are branched (Figs. 2 A and B).

#### *Rooting depth*

Numerous workers, including Freidenfeldt (1902), Weaver (1919), Cannon (1915 and 1925), Anderson (1927), and Salisbury (1925*a*, 1925*b*), have shown that the extent of the root system of a plant and the depth to which the roots penetrate into the soil depend upon a number of edaphic factors such as soil moisture, aeration, texture and reaction. Weaver (1919) has further emphasised that the "working depth" of the root system is of greater importance than its maximal depth. By "working depth" he means "the average depth reached by a large number of roots or branches of the root system, to which depth considerable absorption must take place". The "working depth" normally attained in *M. perennis* is from 10 to 15 cm., but it varies according to the type of soil and the topography of the habitat. For instance, in loose soils

with high organic content (15–20 per cent.) and high water content (45–70 per cent.) as in Purley Beeches, the roots are mostly confined to the upper 10 cm. of the soil. In such cases there is a strong development of the surface feeders

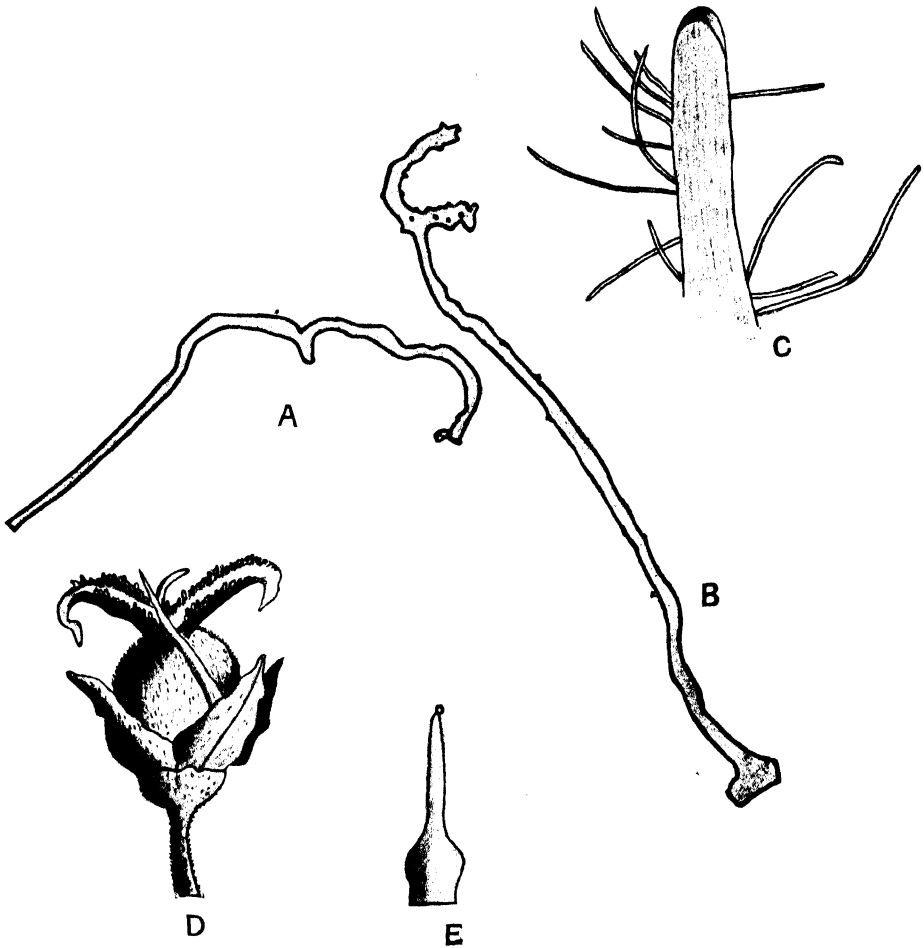


FIG. 2. A and B, branched root hairs of *M. perennis* appearing as forked structures. C, Root of *M. perennis* showing intercalation of new root hairs in between the older ones. D, A female flower with three ovate-lanceolate perianth segments, two subulate abortive stamens transformed into nectaries and a bilobed pubescent ovary surmounted by two large recurved spreading styles with the stigmatic surface exposed on the upper side. E, An abortive stamen of a female flower with rather broadened base which is transformed into a nectary, exuding a drop of sticky liquid at its tip.

and only a few roots penetrate to a maximal depth of about 15 cm. In calcareous clays, on the other hand (with 10–15 per cent. organic content and 30–45 per cent. water content), the greatest development takes place at a depth of 15–20 cm. In the same way, the roots of *M. perennis* growing on a



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hillside, e.g. at Boxhill, often tend to run in the direction of the slope instead of penetrating deeply. It is also interesting to note that, on the whole, the roots on a south-western slope penetrate deeper than those on the northern.

As a result of the examination of the rooting depths of *M. perennis* from more than 200 wild stations in Britain, it has been found that the roots may penetrate to a maximal depth of about 28–30 cm., though they rarely go below 20 cm. The average rooting depth lies between 10 and 15 cm.

### *Experiments on development and penetration in different types of soil*

With a view to finding out how far the development of the root system was influenced by different types of soils the following experiment was performed. Several plants of *M. perennis*, each possessing a long chain of rhizomes and bearing a number of young shoot buds, were dug from an oakwood (*Quercetum roboris*) at Coulsdon. They were brought to the laboratory and planted on February 16th, 1927, in a specially constructed wooden box with glass sides. Five different kinds of soils were packed up side by side in this box. They were loam, peat, leaf-mould, sand and clay. Two plants with their long chains of rhizomes were planted in this box as near the glass surface as possible, so that the various stages in the development of the roots could be followed through the glass. Care was also taken that each soil type received the same amount of water. After a few weeks, new shoots sprouted in each soil type, so that although all the five shoots belonged to one plant yet the root system of each of these newly formed shoots was now growing in a different kind of soil.

At the end of June 1927 the respective development of the five root systems in the five different kinds of soils was carefully studied, and the maximal depths as well as the "working depths" charted on graph paper. Finally, the total dry weight of the roots was determined for each particular soil type. The data are given in Table III.

Table III.

Kind of soil ...	Loam	Peat	Leaf-mould	Sand	Clay
Total dry weight (gm.)	0.37	0.14	0.25	0.21	0.36
Working depth (cm.)	10–15	3–6	5–10	5–10	10–15
Maximal depth (cm.)	28.8	8.5	17	15	25

It will be seen from the above table that the root system of one and the same plant shows considerable variation when grown in different kinds of soil. The difference lies not only in the mode and extent of branching and the total dry weights, but also in the maximal and "working depth" attained by the roots. Thus it may be safely said, since each soil type received the same amount of water in this experiment, that the soil textures or other peculiarities exercise an undoubted influence, direct or indirect, on the penetration and development of the root system of *M. perennis*.

As will appear from Table III the growth of the roots is best in loamy and in clayey soils. In leaf-mould there is a general tendency to the formation of

surface feeders, the roots being mostly confined to the upper 10 cm. of the soil. In sand the branching is rather poor, while in peat the root system is extremely shallow and the growth as a whole is poorest of all.

These results are in general conformity with my observations on the development and penetration of roots in wild stations in nature, the best growth of the root system of *M. perennis* being found in calcareous clay or in loose loam, as at Woldingham or Staplehurst. In hard clay the root development is decidedly poor. In loose humus soils (with high organic and water contents), as at Purley Beeches, the branching is profuse, but the roots are mostly confined to the upper 10 cm. of the soil. In sandy soils, as at Westerham, they show a poor growth, the branching being meagre and the roots very shallow, seldom penetrating below 15 cm. The poorest growth of all was observed in peaty soils. Not only are the roots sparsely branched but they seldom penetrate below 8 cm.

#### *Effect of soil aeration and soil moisture*

Prof. Salisbury (1925*b*) has already called attention to the effect of badly aerated soils on the root development of *M. perennis*. He has shown that in well-aerated calcareous clay, the root system is strongly developed and reaches a depth of about 20 cm., while in badly aerated calcareous clay of fairly high water content (37 per cent.)—the soil reaction being the same in both cases, viz. pH 6.9—the roots are poorly developed and rarely penetrate below 6 cm.

I have repeatedly observed the same phenomenon both during my field work and in the course of culture experiments in the greenhouse. Plants of *M. perennis* growing in the same kind of soil—other factors being the same—possess a far better developed root system in localities where there is no waterlogging and the aeration is fairly good than in situations where the soil is badly aerated and has a very high water content (above 60 per cent.). The roots of this species cannot withstand waterlogging for any length of time. The deleterious effect of excessive soil moisture soon manifests itself by the lateral rootlets turning brown and beginning to decay from the tip backwards, while the root hairs markedly decrease in numbers, thus resulting in a good deal of thinning out of the root system. This is probably due to low oxygen content of the soil atmosphere which would retard respiration by roots and/or high concentration of carbon dioxide in the soil water, which would naturally exert a toxic effect on the root system.

In nature, earthworms play an important part in promoting soil aeration. This has been fully demonstrated by Darwin and more recently by Salisbury, who has shown how the burrows of earthworms make passages down which air and water can easily pass. Besides earthworms birds also disturb and remove the uppermost layers of the soil. In quest of their food wild birds (e.g. pheasants and others) have been frequently observed removing and throwing away with their claws lumps of litter and soil. This would also, to a certain

extent, promote diffusion of gases between the soil atmosphere and the air above.

In wild stations it has been observed that the best growth of the root system of *M. perennis* takes place in soils whose water content ranges from 25 to about 35 per cent.—provided of course the soil reaction is favourable. The “working depth” in such cases is between 10 and 15 cm., and there is a marked development of the finer branching. It has also been observed that roots penetrate deeper in drier soils than in those which have a high water content. This probably also accounts for the greater depths attained on western slopes than on the northern escarpments of hilly regions (see p. 66).

#### *Effect of low soil temperatures*

Low soil temperatures do not, as a rule, seem to exercise any harmful effect on the growth of the root system in this plant, except for a certain amount of retardation which they cause. In severe winters the uppermost layers of the soil are sometimes frozen to a depth of about 10 cm., but the roots and rhizomes of *Mercurialis* occurring in this layer of the soil withstand freezing remarkably well and the plants are invariably able to survive. They resume their normal functional activity at the approach of the favourable season, though the emergence of the aerial shoots and even the production of the leaves and flowers may be somewhat delayed on account of intense cold. The root sap of this plant, therefore, appears to possess marked powers of withstanding temperatures below the freezing-point. As a rule there is a complete cessation in root development in *M. perennis* in mid-winter, but the period of winter rest varies with the climate and altitude (see p. 78).

#### *Effect of soil reaction on the growth of roots*

The rooting depth of *M. perennis* was investigated in numerous localities with soils of varying reaction. It was found that high hydrogen-ion concentration was correlated with shallower rooting and poorer growth than low

Table IV

Locality	Depth of soil sample cm.	pH of the soil	Natural water content %	Working depth cm.	Maximal depth cm.
Boxhill, Pteridetum	0-15	4.5	34	5	7.5
Chiselhurst	0-15	4.7	32	5	8
Boxhill, Taxetum	0-15	5.6	33	10	15
Boxhill, beechwood	0-15	6.4	34	10-13	18
Upper Warlingham, beechwood	0-15	6.4	32	10-12	17.5
Coulsdon, oakwood	0-15	6.6	34.2	10-13	18.2
Orpington, oak hazel	0-15	6.6	35	10-12	18
Boxhill	0-15	6.8	35	12-15	25
Boxhill, hedgebank	0-15	6.9	35	12-15	22
Staplehurst, hedgebank	0-15	7.1	35	12-15	22
Blackbird Wood, Herts.	0-15	7.1-7.2	36	14-15	20-22
Purley Beeches	0-15	7.4-7.6	36	12-14	18
Purley Beeches	0-15	8.2	35	8-10	11

acidity. The best "working depth" was reached in soils of a neutral to slightly alkaline reaction. This will be evident from Table IV.

It will also be seen from the above table that provided the natural water content of the soil remains favourable for its growth the root system responds markedly to the soil reaction it encounters. This latter point is further illustrated in the case of those soils which show a definite stratification in soil reaction. For instance, a Fraxinetum near Woldingham showed a marked stratification in hydrogen-ion concentration as follows:

Soil at 0-10 cm.	...	pH 6.4
Soil at 10-20 cm.	...	pH 5.2
Soil at 20-30 cm.	...	pH 4.8

The roots of *Mercurialis*, as they penetrated into the lower strata, thus encountered a more and more acid reaction, as a result of which downward growth of the roots practically ceased and they could not penetrate much farther. There was, however, a vigorous formation of lateral branches in the upper strata of the soil of which the pH was 6.4.

The effect of soil reaction on the growth of the plant was the subject of a culture experiment (to be described in the next part of this contribution) in which *M. perennis* was grown in a series of jars containing soils of different pH values. At the end of the experiment it was found that all the factors except hydrogen-ion concentration had remained unaltered. The results on rooting depth and dry weight of the root systems are summarised in Table V.

Table V

	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6
pH of the soil	4.0	4.6	5.2	5.6	6.2	6.7
Dry weight of roots gm.	0.11	0.36	0.39	0.52	0.49	0.61
Rooting depth cm.	10.0	11.2	12.3	14.6	15.1	16.4

#### *Osmotic pressure of expressed root sap*

The osmotic pressure of the expressed sap of the roots of *M. perennis* was determined by Barger's method (Barger and Ewins, 1905) as modified by Halket (1913). Varying percentages of cane sugar dissolved in distilled water were used for this purpose.

As a result of numerous experiments it was found that at a temperature of 16° C., 0.7 per cent. of cane sugar just balanced the columns of expressed sap contained in a number of sealed capillary tubes which were fixed on to glass slides with Canada balsam for periodical examination under a microscope. Hence according to the following equation:

$$P = n \times 0.649 (1 + 0.00367 t),$$

the osmotic pressure of the sap at a temperature of 16° C. would be

$$\begin{aligned} P &= 0.7 \times 0.649 (1 + 0.00367 \times 16) \\ &= 0.481 \text{ atmospheres.} \end{aligned}$$

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This result is of the expected order in the case of a plant like *M. perennis* which normally grows in moist shady situations.

### THE STEM

In early spring the apex of the rhizome emerges from the ground in a bent form (cf. Salisbury, 1916). On reaching the light, it straightens out and becomes the erect, unbranched and solitary shoot characteristic of the plant. The erect stem usually attains a height of 15–45 cm. The maximum height recorded by me is 65 cm. and the minimum 8 cm.

The lower internodes of the stem are longer than the upper ones and they bear minute or rudimentary leaves. Each internode has a raised line on either side, running from between the adjacent stipules of the opposite leaves to the centre line of the leaf below. The stems of female plants are generally taller than those of the males. The shoots of plants growing in very bright light or in situations directly exposed to the sun are light green or pale yellow in colour.

*M. perennis* belongs to the "summer-green type" (cf. Salisbury, 1925*b*), and its aerial shoots persist for about 9–11 months. Practically every one of these shoots dies down to the ground early in December and the plants then perennate, mainly by means of their extensive network of underground rhizomes and roots. Sometimes the stems become lanky and are unable to support their own weight. They then assume a trailing habit. This is, however, very exceptional in nature. In very rare cases the stem may also bear weak lateral branches from some of its lower nodes.

The aerial shoot manifests a distinct pH gradient in its expressed sap. The lower part of the stem near the ground-level exhibits a pH value of 5.8–6.0 during the spring, while the uppermost part nearest the apex has a pH value of 4.8–5.1.

The average dry weight of 100 shoots of *M. perennis* picked at random from wild stations ranges from 15 to 20 gm., although in patches of exceptionally vigorous growth the average may be as high as 30–35 gm. per 100 shoots. The ash content ranges from 9 to 18 per cent., the average being somewhere between 12 and 15 per cent.

As will be shown in a later part of this contribution, the dry weight, the height and the ash content of the shoots is considerably affected by various soil factors and by the intensity of the illumination.

### THE LEAVES

A marked feature of the leaves of *M. perennis* is their great variation in form and size. The recognition of this variability is all the more important since leaf form has been utilised by various workers for the diagnosis of varietal types. The leaves are petiolate and the lamina may be oblong, oval, elliptical, ovate-lanceolate or elliptic-lanceolate, the upper leaves being generally narrower than the lower ones. They are mostly rounded at the base and the tip is

pointed, being either acute or acuminate. The margin is crenate-serrate or deeply serrated. Both lower and upper surfaces of the leaves are generally rough or covered with short hairs.

The leaves are opposite, decussate and bistipulate, largest above the middle of the stem. When fully grown they measure from 5 to 13 cm. in length, including the petiole. The lower internodes of the stem are long and bear only minute or very rudimentary leaves; the upper internodes, on the other hand, are shorter, as a result of which the leaves are rather crowded in the upper half. The stipules are membranous, ovate-lanceolate or subulate, and about 2 mm. long.

The leaf characters of *M. perennis* are susceptible to modifications under different environmental conditions. It has been found by experiment that leaves borne on different shoots of a common parent plant, when the shoots are separated and grown in different types of soils such as loam, clay, sand, peat, leaf-mould and chalk, may vary in shape and outline of the lamina, in their general texture, in dentation of the margin, in hairiness and in the length of the petiole. The same phenomenon of leaf variation is observable in nature too, where one can clearly distinguish a number of habitat forms of the types already described on p. 43. These ecads are closely associated with the peculiar conditions of their respective habitats. But it must be remembered that they are by no means definitely fixed forms, being susceptible to alterations under changed conditions of environment.

#### *Sun and shade leaves*

The structure of the assimilating tissues of the leaf of an angiosperm, especially the number of its palisade layers, the depth of its cells, the relative proportion of the palisade and spongy parenchyma, is generally characteristic of a given species. This is not always constant, however, but is subject to modifications if the same species is grown under totally different environmental conditions, as can be well seen in the case of *M. perennis* when we compare leaves growing in shaded localities with those exposed to direct sunlight.

In the shade leaves the epidermis is thin-walled, the mesophyll consists of three rows of cells including the palisade layer, which is made up of rather large rounded cells not so well differentiated as in the sun leaf, the air spaces are relatively large and crystal sacs are frequently present beneath the upper epidermis. The leaves are generally rounded in shape and rather thin. They are broader and usually much bigger than the sun leaves.

In the sun leaves the upper epidermis is distinctly cuticularised, the palisade cells much elongated and displaced at intervals by crystal sacs: the spongy parenchyma alone consists of three layers, and the air spaces are relatively small. The leaves are distinctly thicker, firmer, and more hairy than in the shade form. They are also in most cases very much elongated, often three to four times as long as broad.

*Leaves of male and female plants*

The leaves of the male plants are usually very much elongated, narrower, and smaller than those of the female plants. In the latter they are more rounded, oblong or ovate-lanceolate, being very much larger in size than in the males, and seldom more than twice as long as broad.

In early spring one often finds in wild stations that the leaves of the male plants possess a shining lustre, are upwardly directed and all crowded near the top of the shoot, while those of the female are fully expanded, spreading outwards without casting any shade upon one another. The female plants thus display a well-marked *leaf mosaic* which is associated with the weaker illumination in which they usually grow. Moreover, they tend to form an unbroken screen which cuts off the light from the soil beneath, thus tending to inhibit colonisation by other plants even of taller growth (cf. E. J. Salisbury, 1924).

*Hydathodes*

The upwardly curved apiculus of a leaf tooth in a full-grown leaf of *M. perennis* is surmounted by a water-secreting *epithem-hydathode*. Under conditions of inhibited transpiration, drops of watery liquid containing salts of potassium and calcium are exuded. This sometimes spreads over the upper surface of the leaves and forms a thin shining film.

The hydathodes on the leaves of *M. perennis* readily function when plants are kept overnight under a bell jar in a warm but moist chamber. Early in the morning exudation drops are seen adhering to the margins of the leaves like dew drops.

The secretion of the hydathodes was collected and chemically analysed. It was evaporated to dryness, the dry powdery residue ignited in order to get rid of all organic matter, and the residue then carefully examined. It was found to contain potassium chloride and calcium bicarbonate. The hydrogen-ion concentration of the secretion of the hydathode was greater than that of the expressed sap of the leaves, its *pH* value being 3.9–4.1.

*pH gradient of leaf sap*

The measurement of *pH* value of the expressed sap of the leaves borne on different parts of the shoots showed that the sap of the uppermost leaves is more acid in reaction than that of the older and lower ones. During the early spring the leaves collected from the lower parts of the shoot gave a *pH* value of 5.8–6.0, those from the middle region of 5.3–5.5, those at a higher level 5.0–5.2, whilst the youngest pair at the top gave 4.8–5.0. There is thus a well-marked gradient in the hydrogen-ion concentration of the sap during the spring, when the plants are in a vigorous state of growth and carbon assimilation is in full swing. During the summer, however, the *pH* gradient is not pronounced, probably due to the buffer action of the organic and inorganic colloidal substances which accumulate at this stage in the cells of the leaves.

The *pH* of the expressed sap of the leaves borne in different parts of the stem is now generally found to have a nearly uniform value ranging from 5.3 to 5.5.

On the whole, the youngest leaves usually give a more acid reaction than the older ones. In fact as the leaves grow older and reach the state of senescence, prior to their death, their sap tends to become less and less acid. Bews (1922), working on South African plants, has recorded a similar phenomenon.

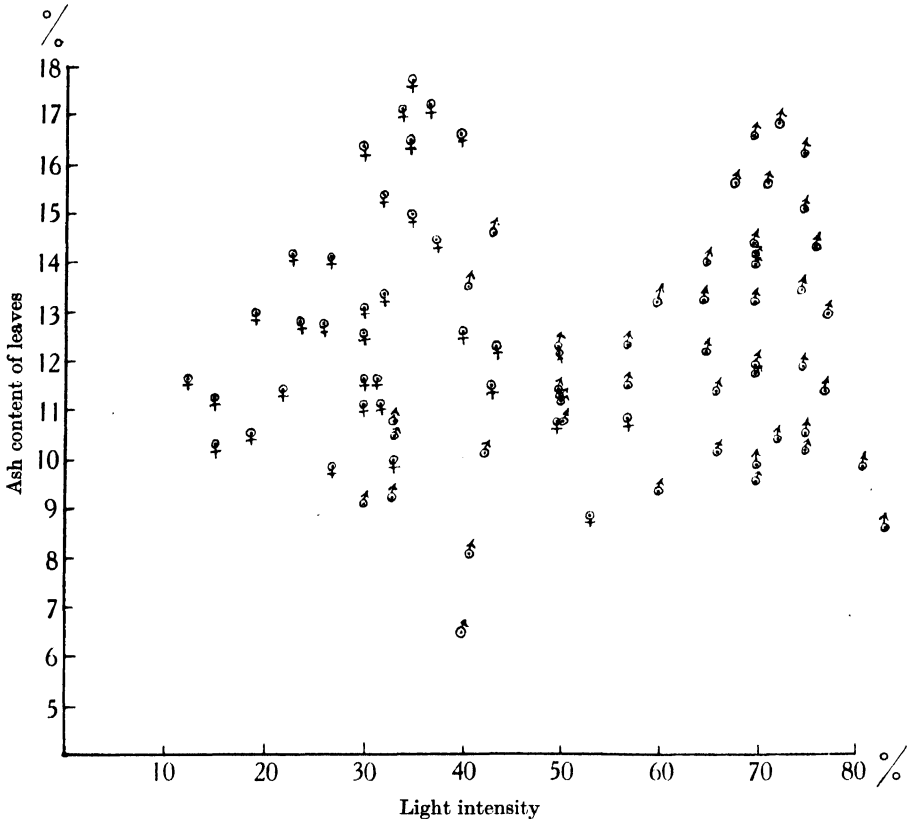


FIG. 3. Graph showing ash content of leaves on shoots of *Mercurialis perennis*. Each locus indicates 100 shoots collected at random. ♂ = male shoots, ♀ = female shoots.

#### *Ash content of leaves*

Leaves were collected from plants growing in different localities in Britain and their ash content was determined in different seasons of the year. It was found that the ash content ranged from about 7 to 18 per cent.

In more shaded situations (i.e. those receiving from 30 to 40 per cent. of full light intensity) the ash content of female plants is generally higher than that of the males. In more lighted areas (i.e. 50–60 per cent.) on the contrary, the ash content of the males is higher than that of the females (cf. Fig. 3).



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There is also a well-marked seasonal variation in the ash content of the leaves of this species, for in individuals of the same sex growing under a specific range of light intensity, the ash content reaches its maximum in spring, after which there is a definite decrease. For instance, the ash content of the leaves of female plants from Woldingham was found in April to be 15.2 per cent., while in August it showed a decline to 10.5 per cent. This decrease in ash content was also noted in about twenty other localities. The decrease in ash content of the leaves of male and female plants of this species appears to be correlated with the production of underground rhizomes and roots during the period from July to September. This is very likely due to the diversion of the elaborated products of metabolism from the leaves to the subterranean parts of the plant where they are now in greater demand. The complex nitrogenous compounds and carbohydrate matter are partly stored up in the tissues of the rhizomes and roots for future formation of reproductive and vegetative organs and partly used up in the current year's growth.

### *Decay and shedding of leaves*

The leaves of *M. perennis* are generally shed in winter. They may fall singly or in pairs, but usually many are shed along with the shoot as a whole. As a rule they die from below upwards, i.e. the lowest pairs of leaves die first and then the upper ones. The individual leaves die from tip to base. Even after death, when the leaf has completely dried up and turned yellow, it often remains attached to the shoot, breaking away when violently shaken by the wind.

### INFLORESCENCE AND FLOWERS

The flowers of *M. perennis* are generally produced before the leaves are fully grown. The male flowers are borne in little clusters of four to seven, grouped in pseudo-spikes of which the apical flower opens first. These spikes arise from the axils of the middle and upper leaves, the glomeruli occupying the upper half of the spike. The male inflorescence generally extends beyond the leaves and its flowers are conspicuous in early spring by their greenish yellow stamens.

The male flowers are either sessile or only shortly stalked, with pedicels 1-2 mm. long. Each flower consists of a greenish perianth of three ovate-acuminate, concave, rather glabrous segments and possesses a variable number of stamens which usually range from eight to twenty, seldom more. Each stamen consists of a biloculate yellow anther and a slender filament. Each anther contains a large amount of pollen, which is extremely light, the smooth grains often floating about with the wind. The pollen grains are sulphur yellow in colour, closely tuberculate, and ellipsoidal in shape. On an average they measure  $39\mu$  long and  $20\mu$  broad. The two globular sacs which are situated upon pale delicate filaments diverge and dehisce upwards. The anther lobes often become indigo blue in colour after the pollen grains are scattered.

Kerner held that the stigmas of the female flowers are receptive at least 2 days before the anthers of the male ones dehisce (cf. Kerner and Oliver, 1895), but my experience is that the male flowers sometimes shed their pollen in the early flowering period before the female flowers are yet ready to receive it.

The female inflorescence is shorter than the male. It may, in rare cases, possess only a single terminal flower but usually it bears two, three, or even four rather remote flowers. Each female flower is distinctly stalked and consists of a perianth which is similar to that of the male flower, being made up of three ovate or lanceolate, acuminate segments, 2 mm. long. There are two subulate abortive stamens with rather broadened bases which are transformed into glandular filamentous nectaries (Fig. 2 E). In the fully grown female flowers these latter often exude drops of sticky liquid from their pointed tips.

As a rule, each female flower has two carpels and the ovary is distinctly two-lobed, but rarely a three-carpelled flower may be met with. The ovary is generally pubescent or covered with bristly hairs. It is surmounted by two large recurved or spreading styles with the stigmatic surface exposed on the upper side. The latter is whitish in colour and has a rough surface due to a large number of fine papillae or projections (*vide* Fig. 2 D). It is also viscid. The two carpels contain each a single anatropous ovule with ventral raphe.

In Britain the period of flowering of *M. perennis* usually extends from the middle of February till the end of May. The flowering attains its height from the middle of March to about the middle of April. Sometimes the plants flower twice in the year—once in the spring and then again in the autumn (cf. George, 1889). I have examined this point carefully and find that autumn flowering is very exceptional among wild plants.

#### *Retardation and suppression of flowering*

Retardation of even complete suppression of flowering may take place, and is brought about by one or more of the following factors:

(1) Low soil temperatures—frozen ground. It has been observed in nature that prolonged low soil temperatures in the places where *Mercurialis* grows, either definitely retards flowering or completely suppresses it. The same phenomenon takes place where there is:—

(2) an excessive amount of water present in the soil (cf. pp. 54–5), or

(3) a very low nitrate content: and lastly when

(4) the intensity of light reaching the ground where *Mercurialis* grows is extremely low, viz. below 4–5 per cent. during the “light-phase”.

#### *Pollination and Fertilisation*

Pollination is effected both by wind and by insect agencies. It used to be held that the genus was entirely wind-pollinated, but recent work has shown that this belief is erroneous. Insects of various types such as butterflies,

moths, bees and ants often visit both the female and the male flowers of *M. perennis* either in quest of nectar or to feed upon the pollen.

It has been recorded by Scott-Elliot (1896) that the honey-bee visits the flowers of this plant. On several occasions and in various localities I have observed bees collecting pollen from the male flowers and nectar from the female. According to the researches of Frisch bees can distinguish yellow and blue, but not red or green. It would therefore seem that bees may be attracted by the yellow filaments and anther lobes of the stamens, by the sulphur-yellow grains of the male flowers, and by the yellowish green colour and nectar of the female flowers. According to Knuth (1899–1904) moths also visit the flowers and play some part in pollination. Recently Hegi (1931) has recorded that insects of various kinds, e.g. night-flying lepidoptera, bees, ants, and small flies effect pollination in this species.

During the course of my ecological work in the field, I have observed on numerous occasions insects, such as bees, butterflies, moths, ants (of a red variety) and flies, visiting both male and female flowers of *M. perennis* and bringing about pollination. I do not, however, consider that this method is in any way universal or very effective on a large scale. My experience is that *M. perennis* is *predominantly* anemophilous and that only a very minor part is played by insect agency. Wind pollination is facilitated in this species owing to the production of a large number of pollen grains and to the styles being rather large and spreading with the stigmatic surface exposed on the upper side. The stigmatic surface is viscid and papillose; hence it easily catches the light pollen grains floating in the air.

There is sometimes a great wastage of pollen grains in this species, due either to heavy rains or violent gusts of wind. As a consequence it may happen that towards the close of the flowering period, i.e. at the end of May or beginning of June, when the female plants still continue to produce fresh flowers, the males have no pollen left in them. The result is that such female flowers remain unfertilised. This naturally causes the withering of quite a large number of female flowers in some localities where owing to certain edaphic influences the flowering in the female plants may have been delayed. This would, of course, result in a great diminution in seed production.

Pollen grains readily germinate on the stigmas, and the resulting pollen tubes make their way to the egg cells by penetrating the micropyle (porogamy), but in many cases fertilisation does not take place, thus resulting in the formation of abortive seeds, as already mentioned (p. 54).

#### THE FRUIT AND ITS EXPLOSIVE MECHANISM

The fruit of *M. perennis* is a two-celled capsule. It has a rather thick pericarp which is covered with warts or bristly hairs. It generally measures 6–7 mm. in breadth and 5 mm. in length.

When the fruit is fully ripe it bursts open with a characteristic sound,

throwing the seeds away with a violent jerk. This explosive mechanism is due to several layers of lignified cells which lie just below the outer epidermis. The hypodermal layer consists of fibres which are placed at an angle of  $45^\circ$  to the axis of the fruit; then comes a layer which is elongated radially, and finally there are two or more layers of cells in which the fibres are at right angles to those of the hypoderm. The result is that during the process of ripening and drying of the fruit, different tissue layers contract in different degrees, so that considerable tension is set up between them. Ultimately the wall gives way suddenly and each valve opens outwards with a violent jerk, ejecting the enclosed seed to a distance of about 3–4 m.

#### DISPERSAL OF SEEDS

The seeds of *M. perennis* possess no special “aids” to dispersal (except perhaps the arillar elaiosomes, the significance of which is rather obscure). But in spite of the absence of any such “devices” as wings, hooks, etc., they are dispersed to some distance from the parent plants. The agencies which bring about this dispersal may be classed under four heads:

(1) *Seeds ejected from fruits.* The forcible ejection of seeds by the violent bursting of fruits is a very effective method of seed dispersal in this species. On examining a very large number of plants in nature, it has been found that plants arising from the germination of seeds generally take 3–4 years before they can produce flowers and viable seeds. Hence if a given plant reaches its fruiting stage, say at the end of 3 years, its seeds would be dispersed to a distance of about 4 m., roughly on the circumference of a circle of which the centre would be the plant itself. These seeds in their turn would germinate and hence at the end of about 6 years the freshly produced seeds of *Mercurialis* would reach new areas situated at a distance of about 8 m. from the first parent plant. No doubt, this is a very slow process of dispersal, but all the same it is quite effective in the long run.

(2) *Occasional gales and violent gusts of wind* sometimes carry seeds of *Mercurialis* along with other litter strewn on the floor of woodlands to great distances, especially when the wind blows downhill over a society growing on a slope.

(3) *Rain water* also occasionally carries seeds of this plant from higher to lower ground.

(4) *Dispersal by ants* is by no means either an important or a universal method in this species. In all my field experience, I have seen only *four cases* where ants carried the seeds of *M. perennis* to a distance of 20–30 m. These were observed at Coulsdon and Staplehurst. Sometimes the ants only carried the shells of broken seeds completely devoid of kernels. My purpose in citing these cases is merely to record the fact that ants do sometimes carry seeds of *M. perennis* to their nests. It may be that they are attracted by the arillar

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elaiosomes mentioned above. If so, this seed would come under Sernander's (1906) class (a) of myrmecochorous plants.

### PROPAGATION BY VEGETATIVE MULTIPLICATION AND BY SEEDS

As is well known, *M. perennis* grows in dense masses on the floor of woodlands and copses, forming either pure stands or occurring in association with other herbaceous plants. This gregarious habit is due chiefly to its great power of spreading over large areas by vegetative multiplication. It has been observed in nature that during the spring and sometimes again in the autumn a large number of young rhizomes are formed. These traverse the ground in all directions at a depth of 2–8 cm. and by their further branching form a dense and extensive network of ramifications. After traversing a longer or shorter distance the apex of each rhizome emerges and forms the unbranched aerial shoot of the plant.

On an average the annual extension of the rhizome from the previous year's root stock covers a distance of about 10–15 cm., although in exceptional cases it may even exceed 40 cm. The number of internodes produced annually varies from two to five. Each node of the underground part of the rhizome produces shoots and adventitious roots and often becomes the centre for the formation of a fresh network of rhizomes. In this way practically every bit of the ground is exploited and a very large number of new plants is produced owing to the decay of the older parts of the rhizomes which formed the connecting links between these newly formed plants and the parent plant body. This decay of old portions of rhizomes and the consequent separation of young plants from the old ones generally takes place at the end of 4 or 5 years. In this way young plants are periodically detached from the older ones and lead an independent existence.

Although *M. perennis* chiefly propagates itself and spreads to new areas by vegetative means, yet it must be emphasised that regeneration by seed is also of great significance because it is a strictly dioecious species. The mingling of the individuals of the two sexes in nature is ensured by the production of new plants of either sex in the midst of a clump of opposite sex by the scattering and germination of seeds described above.

### ASSIMILATORY PERIOD. PERIODICITY AND WINTER REST

The assimilatory period of *M. perennis* usually commences in the south of England about the middle of February and may last till December. The new leaves expand about February 10th, but those of the tree layer under which it grows in woodlands do not as a rule expand till about April 21st, and even then the full development of the leaf canopy is not attained till about May 13th (cf. Salisbury, 1921). This part of the "light-phase" in early spring, i.e. from February till May, is therefore the season of most active growth for *M.*

*perennis*, and its maximum dry weight, height and ash content are attained during this period.

During the summer the growth of the aerial shoots practically ceases and henceforward numerous underground rhizomes and roots are produced, the products of photosynthetic activity being mainly translocated from the leaves to the growing subterranean organs. The ash content of the shoot from June to August shows an appreciable decrease. This decrease in ash content, accompanied by the formation of a large number of fresh rhizomes and roots, points to the translocation of the food materials to the underground parts, where they are partly used up in the formation of new organs and partly stored up for next spring's vegetative and reproductive activity.

During the "shade-phase", i.e. from May till October, the amount of diffuse light that reaches the ground level where *M. perennis* grows in a beech- or oakwood, is generally 4–10 per cent. It may even be less than 1 per cent. in the most shaded parts where only the female plants may, in very exceptional cases, survive. The plant is, however, still able to carry on photosynthesis, but the elaborated organic material is now chiefly stored in its underground parts for the next year's growth and hence the dry weight of the aerial shoots diminishes to a certain extent.

As a rule the entire crop of aerial shoots dies down to the ground in the month of December. It is only in very exceptional cases that the foliage may persist beyond December. This shedding of aerial shoots appears to be dependent to a certain extent upon the degree of illumination received by the plant. For instance, in situations of moderate shade the plant may retain its aerial shoots right up to the next spring while in very dense shade, the shedding may even start early in the autumn.

*M. perennis* exhibits two well-marked periods of vegetative activity; first in the spring and then again in the autumn. The plant becomes very active at these two periods, producing fresh crops of aerial shoots and underground rhizomes and roots. As a rule, it produces flowers and fruits only once a year, but in exceptional cases it may flower a second time in the autumn (cf. p. 75).

The plant undergoes a more or less prolonged period of winter rest which varies in different parts of Europe, according to the climate, topography and latitude of the country. In Britain *M. perennis* usually has 2–3 months of winter rest, viz. from December till February. During this period all growth and formation of new organs ceases, the aerial shoots wither away and are finally shed.

In Central Europe the period of winter rest is generally from 3½ to 4 months, whilst in Russia and Finland it is 6 months (Hegi, 1931). In the latter countries and also in the lower regions of the Alps the aerial shoots are buried under snow for some time, but the remarkably resistant underground rhizomes survive the severe winter conditions.

## 80 *Contributions to the Autecology of Mercurialis perennis L.*

Despite this well-marked periodicity, *M. perennis* may sometimes be induced to grow almost continuously throughout the year. This aperiodic behaviour under artificial conditions was first demonstrated by Diels (1918). I have since observed the same phenomenon in my culture experiments. Even flowering for a second time in the autumn has been induced under culture conditions, the male plants flowering more readily than the females.

### REFERENCES

- Adamson, R. S.** "An ecological study of a Cambridgeshire Woodland." *J. Linn. Soc. (Bot.)*, **40**, 1912.
- Adamson, R. S.** "The woodlands of Ditcham Park, Hampshire." *This JOURN.* **9**, 1921.
- Anderson, V. L.** "Studies of the vegetation of the English chalk. V. The water economy of the chalk flora." *This JOURN.* **15**, 1927.
- Barger, G. and Ewins, A. J.** "Application of the microscopic method of molecular weight determination to solvents of high boiling-point." *Trans. Chem. Soc.* **87**, 1905 (quoted from Halket).
- Bews, J. W.** "The measurement of the hydrogen-ion concentration in South African soils in relation to plant distribution and other ecological problems." *S. Afr. J. Sci.* **19**, 1922.
- Cannon, W. A.** "On the relation of root growth and development to the temperature and aeration of the soil." *Amer. J. Bot.* **2**, 211, 1915.
- Cannon, W. A.** "Physiological features of roots, with especial reference to the relation of roots to aeration of the soil." *Publ. Carneg. Instn.* No. 368, 1925.
- Crocker, W. and Davis, W. E.** "Delayed germination in seed of *Alisma plantago*." *Bot. Gaz.* **58**, 285, 1914.
- Diels, L.** "Das Verhältnis von Rhythmik und Verbreitung bei den Perennen des europäischen Sommerwaldes." *Ber. deutsch. bot. Ges.* **36**, 337, 1918.
- Freidenfeldt, T.** "Studien über die Wurzeln kräutiger Pflanzen." *Flora*, **91**, 115, 1902 (quoted from Skene).
- George, F. J.** "Autumn flowering of *Mercurialis perennis*." *J. Bot.* **21**, 376, 1889.
- Gillot, P.** *Recherches chimiques et biologiques sur le genre Mercurialis*. Nancy, 1925.
- Guppy, H. B.** "Plant distribution from an old standpoint." *Victoria Inst. Trans.* April 8th, 1907.
- Halket, A. C.** "On various methods for determining osmotic pressures." *New Phytol.* **12**, 1913.
- Hegi, G.** *Flora von Mittel-Europa*. Munich, 1931.
- Icones Florae Formosa*, **5**, 199, 1915.
- Kerner, A. and Oliver, F. W.** *Natural History of Plants*. English ed. **1**, ii, p. 403.
- Knuth, P.** *Handbuch der Blüten Biologie*. Leipzig, 1898-1904.
- Krasan, F.** In *Oest. bot. Z.* **15**, 217, 1865 (quoted from Pax).
- Lehmann, E.** "Temperatur und Temperaturwechsel in ihrer Wirkung auf die Keimung lichtempfindlicher Samen." *Ber. deutsch. bot. Ges.* **29**, 577, 1911.
- Magrou, R.** "Symbiose et tuberisation." *Ann. Sci. nat. (Bot.)*, **10**, No. 3, p. 181, 1921 (quoted from Gillot).
- Mukerji, S. K.** "New variety of *Mercurialis perennis* L." *J. Bot.* **65**, 1927.
- Pax, F.** "*Mercurialis* formes Pax et K. Hoffm." in Engler, A., *Das Pflanzenreich*, **4**, 147, VII, pp. 270-82, 1914.
- Russell, E. J.** *Soil Conditions and Plant Growth*. 5th ed. Longmans, 1927.
- Salisbury, E. J.** "The emergence of the aerial organs in woodland plants." *This JOURN.* **4**, Nos. 3 and 4, 1916.
- Salisbury, E. J.** "The oak-hornbeam woods of Hertfordshire." Parts I and II, *This JOURN.* **4**, 1916; Parts III and IV, *ibid.* **6**, 1918.
- Salisbury, E. J.** "Phenology and habitat with special reference to the phenology of woodlands." *Quart. J. R. Met. Soc.* **47**, 200, 1921.
- Salisbury, E. J.** "The effects of coppicing as illustrated by the woods of Hertfordshire." *Trans. Herts. Nat. Hist. Soc.* **13**, Part I, 1924.
- Salisbury, E. J.** "The incidence of species in relation to soil reaction." *This JOURN.* **13**, 1925 (a).
- Salisbury, E. J.** "The Structure of Woodlands." *Festschrift Carl Schröter*. Zurich, 1925 (b).
- Scott-Elliot, G. F.** *Flora of Dumfriesshire*, p. 152, Dumfries, 1896.

- Sernander, R.** "Entwurf einer Monographie der europäischen Myrmekochoren." *K. Svenska Vetenskapsakad.* **41**, 1906 (quoted from Skene).
- Skene, Macgregor.** *The Biology of Flowering Plants.* London, 1926.
- Tansley, A. G.** "On competition between *Galium saxatile* L. (*G. hercynicum* Weig.) and *Galium sylvestre* Poll. (*G. asperum* Schreb.) on different types of soil." *This JOURN.* **5**, 1917.
- de Vries, H.** "Über künstliche Beschleunigung der Wasseraufnahme in Samen durch Druck." *Biol. Z.* **35**, 161, 1915 (quoted from Skene).
- Watt, A. S.** "On the ecology of British beechwoods, with special reference to their regeneration. Parts I and II." *This JOURN.* **11**, 1923.
- Weaver, J. E.** "The ecological relations of roots." *Publ. Carneg. Instn.* No. 286, 1919.
- Winkler, A.** "Über die Keimpflanze der *Mercurialis perennis*." *Flora*, **63**, 339-44, 1880 (quoted from Gillot).
- Woodhead, T. W.** "The ecology of woodland plants in the neighbourhood of Huddersfield." *J. Linn. Soc. (Bot.)*, **27**, 1906.



# STUDIES IN THE ECOLOGY OF WICKEN FEN

## III. THE ESTABLISHMENT AND DEVELOPMENT OF FEN SCRUB (CARR)

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*(With Plates IV and V and fourteen Figures in the Text)*

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### I. INTRODUCTION

At the outset of our ecological investigations on Wicken Fen it was felt that numerous and varied problems surrounded the processes of bush establishment and of the development of scrub (fen carr) subsequently. At once, therefore, in 1923, two areas on the Fen were fenced off, surveyed, marked and mapped for their bush population, with the object of determining by remapping in

later years the progress of vegetational change. These areas have since been carefully remapped. A similar permanent transect set up in 1929 has been remapped in 1935, and at various times throughout the period from 1923 experiments on dispersal and establishment have been performed in field and laboratory as occasion offered. It is the record of this work of systematic observation and experiment which forms the core of the present account, though it is naturally supplemented and extended by generalised field observations made more casually.

The greater part of the observations are my own, but I owe thanks to J. S. Turner for help with the bird dispersal experiment (p. 91); K. Saw of Downing very efficiently established and first mapped transect C in 1929; F. R. Bharucha determined the germination of seedlings quoted on p. 90; the work of mycological research students working under F. T. Brooks in the Cambridge Botany School is separately acknowledged in the sections on the die-back of *Rhamnus frangula* and on the infection of *Rhamnus* by *Puccinia coronata*. To all these contributors, and to the students and laboratory assistants who have helped me, often under trying conditions, with this work on the Fen, I offer my very sincere thanks.

## II. EVIDENCE OF THE PROGRESS OF BUSH COLONISATION

### (a) *Communities invaded*

In earlier publications (Godwin, 1931, Godwin and Bharucha, 1932 and Godwin and Tansley, 1929) a schema was given showing the major plant communities of Wicken Fen in their presumed successional relations, and it has been stressed that although bush colonisation becomes possible at an early stage in the prisere—probably in *Cladietum*—yet almost always crop taking at intervals of three years or less prevents successful bush establishment and initiates deflected successions. Communities so produced are dry enough to carry bushes and do, in fact, become freely invaded by them when the cutting is suspended, thus initiating what are really secondary successions. The chief types of community on the deflected successions have been described as mixed sedge (*Cladio-molinietum*) which is cut at intervals of three years, and as litter (*Molinietum*) which is cut at intervals of one year only. So much the greater part of Wicken Fen is, in fact, covered by these artificially produced communities that it is bush colonisation in them with which this paper is chiefly concerned. A third type of community also invaded by bushes is the open ground produced by felling adult fen carr, but there has been no satisfactory opportunity of describing this.

### (b) *Water-level relationship*

It has already been shown that the lower limit of bush colonisation on Wicken Fen appears to be round about -10 to -20 cm. below Fen Zero Level—an arbitrary plane to which the movements of the Fen water table have also

been related (2). The Fen at this level is often submerged for long periods in the winter but it is well above water-level in summer. A simplified diagram representing this relationship is shown in Fig. 1.

Air photographs of the Fen taken in 1929 show parallel disposition of young bushes along the ridges left between the furrows made by former peat cutting. The furrows are too low and too wet for bush establishment.

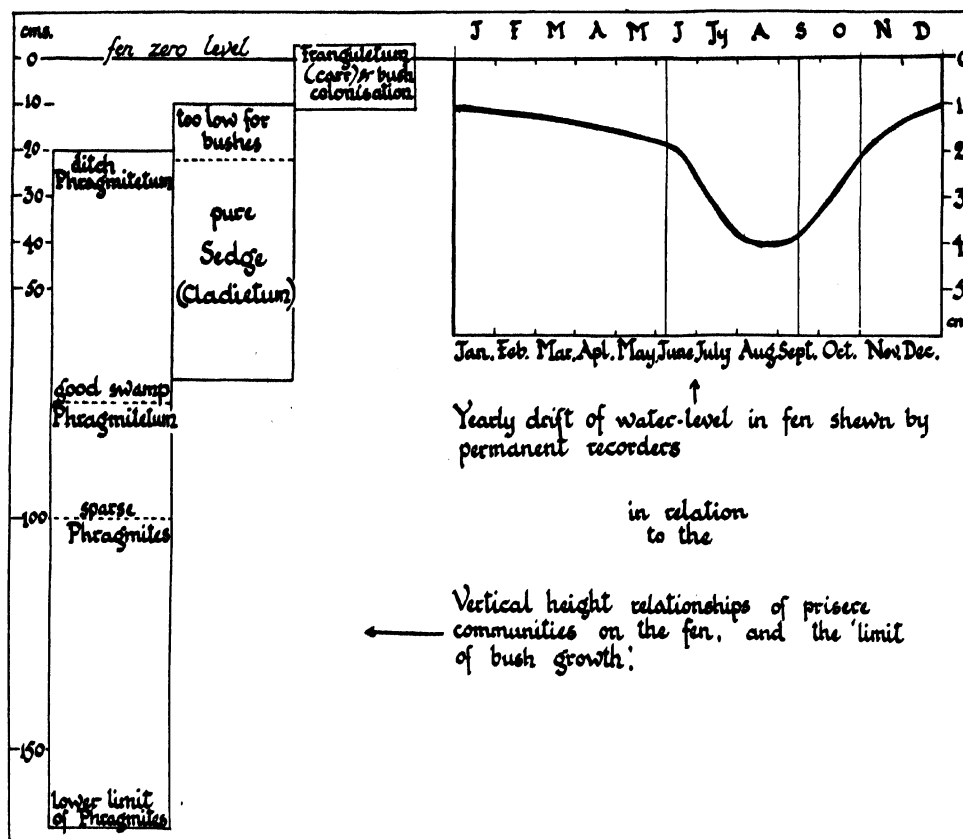


FIG. 1. Diagram showing the vertical height relationships of Fen communities and on the same scale the yearly drift of the water table height in a year of average rainfall. The "limit of bush growth" (too low for bushes) will be seen to be at or below water-level for a large part of the winter and spring, but to be well above it in summer.

### (c) Transect B

The situation of this transect is shown in Fig. 2. It was established in 1923 in a community of typical mixed sedge which has since been left uncut. During the war the area had been cut at more frequent intervals than three years, and this was reflected by a sparse entry of *Carex panicea* and *Juncus obtusiflorus* into the vegetation, but it has not been cut since 1918 and it is probable that the beginnings of bush colonisation date from this time, though

cut stools of earlier date may also be present. The belt is 1 m. wide and 40 m. long. In it were mapped the outlines of all bushes over 0.5 m. high, and their heights were also recorded. From these data the plans and diagrammatic

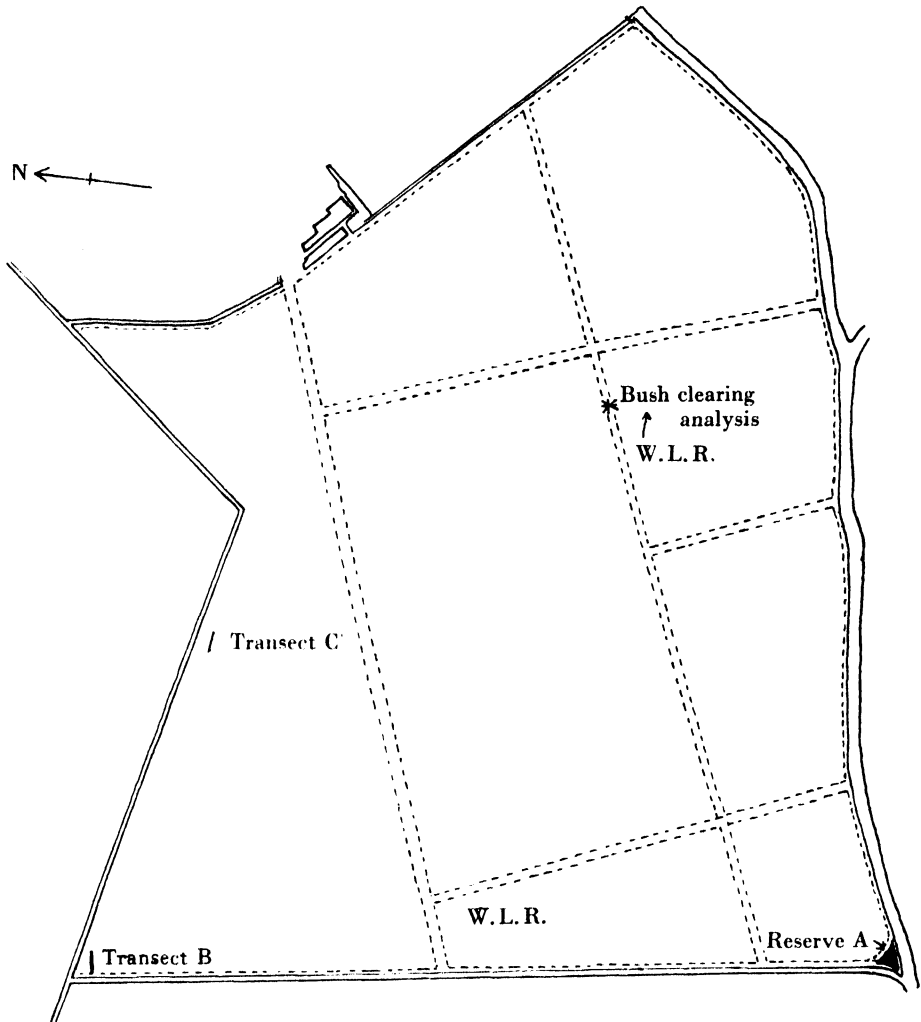


FIG. 2. Map of Wicken Sedge Fen showing the situation of the various permanent and temporary observation areas discussed.

transects of Figs. 3 and 4 have been constructed. The recording was carried out on the following dates: July 26, 1923, June 1, 1927, and July 27, 1931.

The bush species represented are *Rhamnus frangula*<sup>1</sup> (*Frangula alnus* Mill.), *Rhamnus catharticus*, *Salix cinerea*<sup>1</sup> (*S. atrocinerea* Brot.), *Viburnum*

<sup>1</sup> Throughout this paper the older names have been retained for these species because they were employed in making all the earlier records.

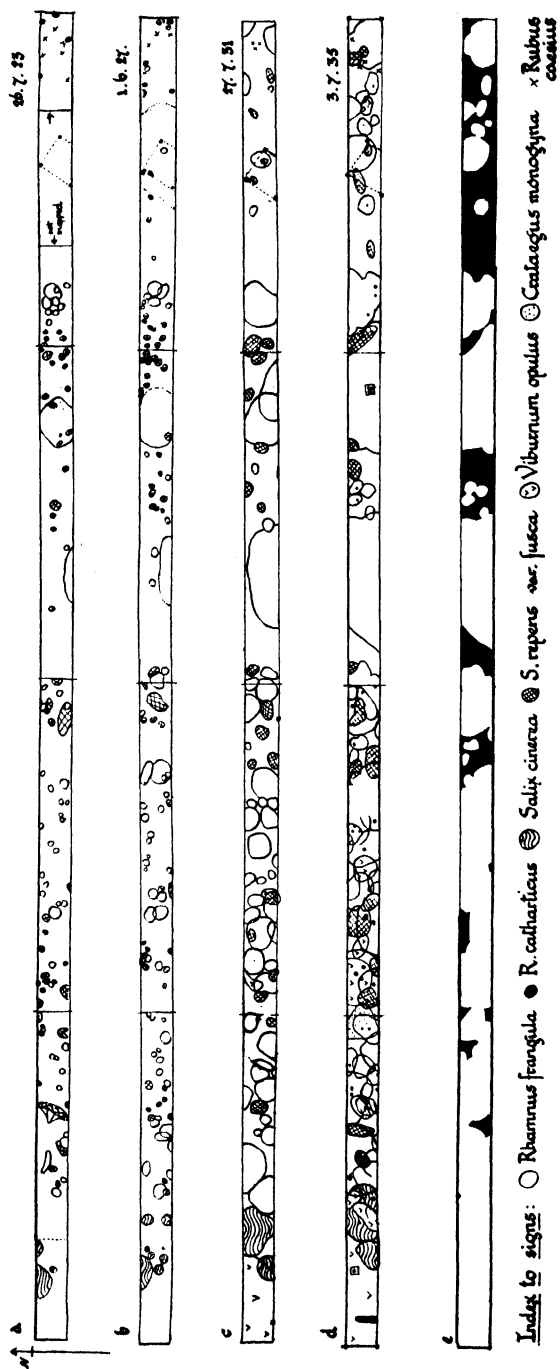


FIG. 3. Belt transect B, remapped over a period of twelve years, showing the rapid progress of bush establishment in a mixed sedge area after crop-taking ceases. *a*, *b*, *c* and *d* show bush outlines at the four mapping periods, 1925, 1927, 1931 and 1935. *e* is taken from the 1935 mapping, and the black area shows the ground still uncovered by bushes (*Salix repens* var. *fusca* not reckoned as a bush). The transect is 40 × 1 metres.

*opulus* and *Salix repens* var. *fusca*. The last-named species is a normal component of mixed sedge and plays no part in the development of mature carr, from which indeed it is quite absent. It will be seen from the profile transects of Fig. 4 that 1 m. represents the maximum general height reached by this species, and though the bushes have coalesced in the time between 1923 and 1931 and have increased in height it seems evident that it will remain subordinate to the other bush species.

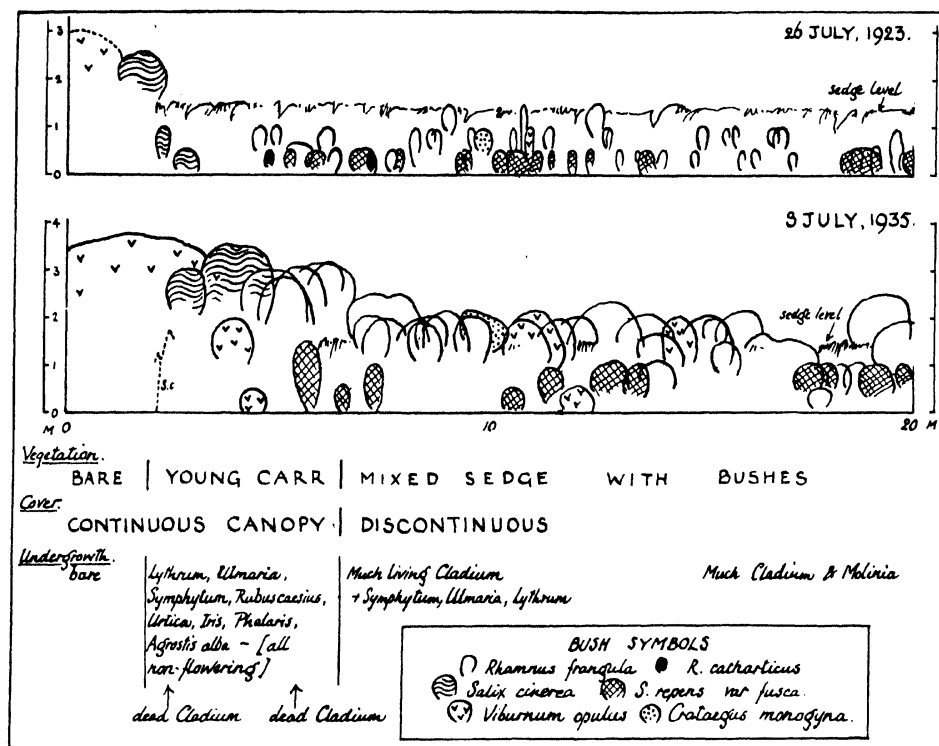


FIG. 4. The western half of belt transect B, reconstructed in profile from the maps of Fig. 3 and from field notes, to show changes between 1923 and 1935 in an area of mixed sedge left uncut since about 1918. The general height of the sedge vegetation is shown at 1.5 metres. The notes on vegetation, bush cover and undergrowth refer to the 1935 record. Though the other bushes are now growing above sedge level, *Salix repens*, var. *fusca*, a true sedge associate, still remains below this level. S.c. = dead *Salix cinerea*.

In comparing the bush growth of the successive phases it is important to recognise that the outlines illustrate merely the plan of the erect shoots separately recognisable. Most of the Fen bushes send up numerous trunks from each stool, but it is not practicable to trace each vertical shoot to its base, nor to record bushes less than 50 cm. high. Moreover, as the bush heads increase in size their weight causes the trunks to bend over and alter the position of the head of foliage on the transect. It is this which has been responsible for

the sudden appearance of *Viburnum* across the western end of the transect: branches from a bush just outside the transect have bent over it.

These difficulties preclude too close deduction from the plans: it is not possible, for example, to state changes in the number of individual bushes. Nevertheless, examination will show a small degree both of establishment of new bushes from one plan to the next, and also disappearance.

The major feature of bush establishment quite clearly shown is the rapid rate of extension of the bush crowns and their coalescence into larger masses. A very striking case of the lateral extension of a bush clump is shown about 23 m. from the west end of the transect—about 70 cm. radially in eight years. It seems probable that the bulk of the bushes shown in the 1931 plan date from 1918, when the last sedge crop was taken, and the plans give an idea of the rate of formation of closed scrub canopy after releasing mixed sedge from crop taking. This is probably governed largely by the initial density of establishment in the early phases of more open sedge growth in the first year or two after the cessation of crop taking. Bush establishment was denser in the western half of the transect (nearer the fringe of tall old bushes left uncut by Drainer's Dyke), and the profile transects (Fig. 4) show that already a small area which was open sedge in 1923, had become, in 1935, young carr with a ground flora characterised by species quite different from those of the *Cladio-molinietum*. In this limited area continuous bush canopy has been produced in less than twenty years from ecesis of the bush population. The sparse initial scatter in the eastern half of the transect will apparently cause a much longer time to elapse before the phase of closed bush canopy is reached. The profile transects strikingly illustrate the vertical growth of bushes between 1923 and 1935. They show that at the former date almost all the bushes are just up to, or below, the level of the sedge vegetation, whereas at the later date the bulk of them have exceeded it. This certainly illustrates the method and rate of transition from vegetation dominated by *Cladium mariscus* and *Molinia coerulea* to vegetation dominated by bushes.

A further feature of interest is the great preponderance of *Rhamnus frangula* over all the other bushes. This is a very general feature of bush establishment over the whole of Wicken Fen, and forms the subject of special comment in section III of this paper.

Striking change in the herbaceous vegetation is limited to the western end of the permanent transect: the permanent quadrat which it includes is in the area least heavily invaded by bushes and shows, as would be expected, no effects of progressive bush establishment.

#### (d) *Bush-clearing analysis*

The phase of bush development into which transect B will soon pass may be represented by an area of 50 sq. m. in plot 576 of the Fen which was examined in 1928 with the help of M. E. Godwin and A. H. K. Petrie. It consisted of

scrub in which the bush canopy had become continuous but which still showed irregular bush distribution, persistence of living *Cladium*, *Phragmites* and other plants of the mixed sedge, though showing also their local destruction. The area was in process of being clear cut for a new fen drove, and having been previously measured out, all the bushes cut from the area were piled up together for closer examination. As will be seen from Table I, a large number of useful indices were chosen and measured for each bush. They yield a good general picture of bush composition at this stage of development. There are about 1.4 living bushes per square metre, though each stool has an average of four major trunks, so that there are five to six living shoots per square metre. Already, whatever may be the cause, there is a considerable proportion of dead bushes, mostly *Rhamnus frangula*, amounting to 0.4 per square metre, and the density of dead shoots (often on living stools) is much higher, 2.2 per square metre. This dying out certainly indicates a major part of the mechanism of the next phase of bush development—internal competition and sorting out of the bush population. It will be observed that the general bush height is about 2.3 m., though some reach up to 3.2 m. The greatest age, estimated by ring counts, is 24 years, though much younger bushes are also present. Since the average age of the dead and dying bushes is 15 years it is clear that their death is not simply a matter of old age. The youthfulness of the bush community is shown by the persistence not only of living *Cladium* but also of *Salix repens* var. *fusca*, which is, however, much drawn out and obviously succumbing. The carr-forming bushes are limited to the two species *Rhamnus frangula* and *R. catharticus*, and here as in transect B there is a vast preponderance of the former.

Table I

Analysis of an area of 50 sq. m. in a late stage of bush colonisation	<i>Rhamnus frangula</i>	<i>Rhamnus catharticus</i>	<i>Salix repens</i> var. <i>fusca</i>	Totals for all bushes
Living bushes	67	1	4	72
Living shoots	266	14	13	293
Living shoots per bush	4	—	—	4
Living bushes per sq. m.	1.3	0.02	—	1.4
Living shoots per sq. m.	5.3	0.3	0.26	5.8
Dead or partly dead bushes	22	—	1	23
Dead shoots	111	—	1	112
Dead shoots per bush (dead or dying)	5	—	—	5
Dying or dead bushes per sq. m.	0.4	—	—	0.4
Dead shoots per sq. m.	2.2	—	—	2.2
Average age of dead and dying bushes (yrs.)	15	—	—	15
Average age of living bushes (yrs.)	12.4	4	6	12.3
Maximum age of bushes (yrs.)	24	4	8	24
Average height of bushes (m.)	2.35	1.9	1.4	2.3

In comparison with transect B the age counts appear to show somewhat more rapid establishment of the phase of continuous bush cover and the initiation of local killing out of *Cladium*. The rates are, however, of the same order. The density of bushes on the ground is also similar in the two cases. The analysis of bush ages in the bush clearing seems to show that there the establishment of seedling bushes continued over many years (cf. average age



of living bushes 12·4 years and maximum age 24 years): this is in contrast to the heavy initial establishment in transect B.

### III. ESTABLISHMENT OF *RHAMNUS FRANGULA* AND *R. CATHARTICUS*

Both in transect B and the bush-clearing analysis there has been evident an overwhelming preponderance of *R. frangula* in the seedling bushes. This has been established by observation everywhere on the fen, and it is extremely well shown in the map of the north-east portion of Reserve A (Fig. 6). This preponderance is maintained even in the immediate neighbourhood of large clumps of mature bushes of other species, such as *R. catharticus* and *Salix cinerea* in Reserve A, and it is the more remarkable since the mature stages of carr development appear to be dominated by *Rhamnus catharticus* and not *R. frangula*. Facts in support of this view of the nature of mature carr have already been given (Godwin and Tansley, 1929), and its acceptance at once raises two questions of major importance: (a) what are the factors responsible for the seedling preponderance of *R. frangula*, and (b) what is the mechanism of the replacement of *R. frangula* by *R. catharticus* in the development of mature carr? Consideration of these problems forms a large part of the present paper, and the first of them we may consider at once.

#### (a) *Fruiting and age of bushes*

In both species the fruit is a succulent drupe and contains hard stones: these are usually two in the case of *R. frangula* and three in *R. catharticus*, so that here the advantage in seedling production lies rather with the latter species. No exact observations have been made, but it seems unlikely that there is any large difference between the two species in respect of either the numbers of fruits borne on bushes of equal age, or in the age at which fruit is first borne. Both species are very prolific at Wicken and bear fruit very young.

#### (b) *Germination*

Stones expressed from the fruits in September, when they first become ripe, germinate quite readily, giving 90–100 per cent. germination in both species. Where the fruits or stones have been thoroughly dried for some time Bharucha found the germination power was very greatly reduced. It could, however, be restored by cutting through the outer case of the stones before sowing, and here again no substantial difference was recognisable between the two species. However, stones collected and kept dry from September 1933 and sown in January 1935 showed high percentage germination of untreated *R. catharticus* compared with that of *R. frangula*.

#### (c) *Soil acidity*

It is generally found in this country that *R. catharticus* is characteristic of dry calcareous soils, especially the chalk, and *R. frangula* of acid sandy or silty soils, so that the view has developed that the one is substantially a

calcicole and the other a calcifuge. Their presence together on the Wicken Fen peat opposes this view, but it was suggested that possibly conditions of acidity in the surface peat determined the early predominance of *R. frangula*, whilst the general alkalinity of the deeper peat determined that only *R. catharticus* could in the end survive.

Careful and extensive observations were made by R. H. Mobbs on the acidity of the soil round the root systems of seedlings of *R. frangula* in many parts of the fen. His results (1932) show that for seedlings of 5–30 cm. height the root systems are in soil varying from pH 6.5 to 8.3 (average 7.5), and only seedlings of less than 5 cm. rooted in the top cm. or so of surface litter are rooting in strata at all acidic in character. Even here the range is but from pH 6.0 to 7.5 and the mean 6.7. It is known that seeds germinate satisfactorily in alkaline peat, and on sand or filter paper watered with alkaline tap water. *R. catharticus* does equally well under these conditions, and it must be concluded that no advantage lies with *R. frangula* by surface soil acidity favouring early seedling establishment.

#### (d) *Dispersal by birds*

It would be expected from the succulent fruits that bird dispersal would be the rule for both species of *Rhamnus*, and this, to some degree at least, is true. The fruit crop ripens during September, and during this time begins the annual autumn visitation of the fen by large flocks of migratory fieldfares (*Turdus pilaris*). These birds settle in vast numbers in the bush vegetation and appear to feed there. Certainly at this time their excreta on the sedge and reeds is plentiful and is always stained purple, presumably by the abundant pigments of the *Rhamnus* fruits. Differential bird dispersal offers an obvious possibility of advantaging one species of *Rhamnus* against the other, and one or two observations appear to favour such an explanation. Thus in the winter months when all the *R. frangula* bushes are bare save for occasional mummified fruits, there is still an abundance of dried berries on the *R. catharticus* (as also, incidentally, on *Viburnum opulus*). The suggestion that this is due to a preference of the birds for *R. frangula* fruits is partly supported by an observation of Woodruffe-Peacock (1918): "I found in the long frosts of 1895, 1916 and 1917 that these birds (blackbirds) never turn for food to the berries of this species (*Rhamnus catharticus*) till the late spring when all other fruits are exhausted."

The following experiment was made in order to determine the actual removal of fruits from the bushes by birds.

In late September 1932 two adjacent bushes, one of each species of *Rhamnus*, were selected for their similarity in size and shape. They were about 7 ft. (2.1 m.) high. The fruits on each were counted—branch by branch being marked off by wool as soon as once reckoned. The fruits were just ripe and few had yet fallen or been removed. Below each bush a large bag of sacking

9 ft. (2.7 m.) square was suspended from stakes and was carefully sewn round the bush stems a foot or so above ground-level. The sacking extended well beyond the bush crown so as to catch even berries detached by strong winds and blown sideways, but it is possible that a few may have been lost in this way. (However, the *R. frangula* bush was just to leeward of the *R. catharticus* bush and the sacking round the *R. frangula* caught no *R. catharticus* fruits blown from the windward bush.) The general appearance was that shown in Fig. 5, save that litter of dead grass and sedge was piled on the canvas to make

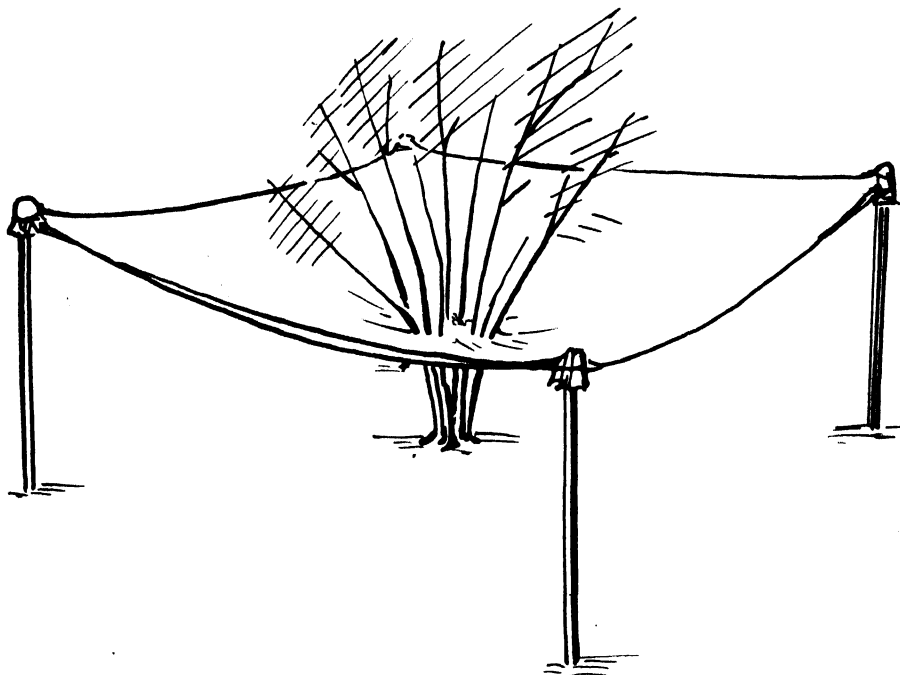


FIG. 5. Figure to show the arrangement of sacking round the *Rhamnus frangula* and *R. catharticus* bushes in the experiment to determine the relative importance of bird dispersal for the two species.

it less obvious to the birds. At this time large flocks of fieldfares had just begun to appear on the fen. At the end of December, when the *R. frangula* bushes all over the fen were bare of fruit, the fruits on the two bushes were counted again, together with the fruits fallen into the sacking. These had to be carefully picked out from the litter, and they included a large number of stones escaped from the dried fruits or defaecated by birds on the spot. These were dealt with by reckoning two stones of *R. frangula* to one fruit, and three of *R. catharticus* per fruit. The results are given in the table below: it should be noted that the *R. frangula* bush was quite bare of mature fruits and the *R. catharticus* bush almost so.

	<i>R. frangula</i>	<i>R. catharticus</i>
Fruits on bush, Sept. 27, 1932	1804	1455
Fruits collected from sheet, Dec. 24, 1932	1118	431
Fruits represented by stones in sheet	150	20
Fruits disappearing (including a few still on <i>R. catharticus</i> bush)	536	1004

These figures are only approximate, but they are nevertheless sufficiently striking. It does not matter whether or no the fruits reckoned from stones in the sheet are considered to have been bird dispersed: it is clear (a) that if there was differential removal from the neighbourhood of the birds due to bird dispersal the advantage lies rather with *R. catharticus* than with *R. frangula*, and (b) that the rapid clearing of the *R. frangula* bushes of fruit is due in large part merely to the natural falling off of the fruit when ripe. The fruits of *R. catharticus* are shed far more slowly. It might also be said that many more *R. frangula* fruits fall to the ground than are eaten by birds, but the isolated nature of the observation and the peculiar effects of the apparatus forbids too general a conclusion. At the same time the result is a sufficiently striking warning against the assumption that all succulent fruits, or even most of them, do in course of time get dispersed by birds. It also seems to show that it is not here that the distinction between seedling establishment of *R. frangula* and *R. catharticus* is to be found.

(e) *Dispersal by mice*

It is not usual to consider the influence of rodents upon the dispersal of species with succulent fruits, but the results of the last-mentioned experiment suggested that so large a proportion of the *Rhamnus* fruit crop is not bird distributed that other factors might be of unsuspected importance. Further, it had already been observed that when field mice (*Mus sylvaticus*) had made nests in the water-level recorder case (Godwin, 1931) on the Fen they had brought to it stones of *R. frangula*, and these had been eaten except for the characteristic arillar portion.

On September 28, 1933, therefore, an experiment was set up in the Molinietum by the water-level recorder, designed to show the extent to which mice and birds respectively will take the fallen fruits or stones of the two *Rhamnus* species. Six shallow wooden trays were disposed as follows:

- (a) 100 stones each of *R. frangula* and *R. catharticus*:
  - (1) Tray on post 4 ft. (1.2 m.) above ground.
  - (2) Tray on ground in litter.
  - (3) Tray on ground in litter but covered with wire netting.
- (b) 100 fruits each of *R. frangula* and *R. catharticus*:
  - (1) Tray on post 4 ft. (1.2 m.) above ground.
  - (2) Tray on ground in litter.
  - (3) Tray on ground in litter but covered with wire netting.

It was intended that 1*a* and 1*b* should be accessible only to birds, 2*a* and 2*b* to both birds and mice, and 3*a* and 3*b* to neither birds nor mice. (It turned out that the wire was, in fact, not of fine enough mesh to exclude mice.)

By November 1st the trays gave the following results:

	Numbers left		Notes
	<i>R. frangula</i>	<i>R. catharticus</i>	
(a) Trays with stones:			
(1) Open tray on post	67	54	Probably inaccessible to mice—no excreta. Therefore possibly removed by birds. Unlikely to have been by wind
(2) Open tray on ground	0	0	Abundant mice excreta and remains of stones
(3) Wired tray on ground	1	3	Do.
(b) Trays with whole fruits:			
(1) Open tray on post	200		No bird removal
(2) Open tray on ground	68		Most of remainder large and succulent: probably <i>R. catharticus</i> . Mice excreta and remains of stones
(3) Wired tray on ground	127		Do.

It is perhaps not striking that birds have not taken succulent fruits from an open tray in the fen, but it is more remarkable in view of the fact that quite a large number of stones disappeared from a similar exposed tray, probably by bird agency. A very striking effect indeed is, however, the removal within a month of *all* the stones from the open tray (and of all but four stones from the wired tray) left on the ground. In each case it was evident that mice were largely responsible. In the same way the losses of whole fruits were evidently due to mice, though it seems likely that the mice only eat the stones when they become exposed by the drying or decay of the mesocarp. The untouched fruits were all intact, large and succulent, and seemed to include more *R. catharticus* than *R. frangula*. This effect could, however, be only a transitory one, and whether we consider the mice as destroying the stones, or, possibly, as transporting them, they do not appear to differentiate between the two *Rhamnus* species.

The possibility of mice transport was clearly shown in the Botany School field classes of 1934. In recently cut ground several clumps were seen of tightly packed *R. frangula* seedlings about 10 cm. high. Dr A. S. Watt suggested that these might be mouse stores, and digging showed at once that this was indeed what they were. Collections of stones buried and forgotten or deserted had germinated together, piercing the few centimetres of peat from the mouse run to the surface. There were from thirty to fifty seedlings in each small clump.

At the time when the tray experiments were begun seven boxes of peat were planted with ripe *Rhamnus* stones, fifty of each species. Three boxes were brought back to the Cambridge Botany School, two were embedded to ground-

level in mixed sedge vegetation of the Fen and two were similarly embedded in an adjacent clearing. By August 8, 1934—10 months later—the boxes contained the following living seedlings:

	No.	<i>R. frangula</i>	<i>R. catharticus</i>	
Botany School	1	38	43	
	2	36	36	
	3	41	31	
Fen (mixed sedge)	4	}		0
	5			0
Fen (clearing)	6	}		3
	7			4

These results not only show the high capacity of seeds of both species to produce healthy seedlings given favourable conditions, but also the importance of the adverse factors on the Fen. In the boxes on the Fen there was no trace of dead seedlings—nor was it possible to recover the original stones from the peat. At the same time there were on the peat surface gnawed husks of some stones, and it seems probable that though planted below soil-level they had been discovered and eaten by mice. Probably the loosening of the surface peat by frost action, which is marked, had facilitated this, but there is no means of knowing what other factors may have been involved or their magnitude in relation to the mice factor.

(f) *Numbers of seed parents*

All the foregoing experiments have failed to reveal any reason which accounts for the different status of the two species of *Rhamnus* in seedling establishment. Though the possibilities of experiment are by no means exhausted, especially with regard to early post-germination stages of establishment, yet one is forced to consider how far the circumstance may be due to local historical causes rather than to permanent and general biological factors. It is certainly true that at the present time the frequency of *R. frangula* seed parents on the Fen is vastly greater than that of *R. catharticus* seed parents. It is true that the bulk of the former are very young and of the latter older, but nevertheless the same preponderance of *R. frangula* seed parents may well have lasted for many years past, especially since little old carr dominated by *R. catharticus* can have been suffered to exist during the former days of more intensive crop cutting on the Fen. This supposition, it is true, does not explain the initial discrepancy between the numbers of seed parents of the two species; this might have happened by chance or by some unsuspected factor such as human selection. At the moment the relative bulk of seed available does clearly distinguish the two *Rhamnus* species on Wicken Fen, and it has not been possible to discover any general biological factor acting in the same sense.

## IV. RESERVE A (EARLY STAGES OF CARR FORMATION AND EXTENSION)

In 1923 a large area, named Reserve A, was set aside for the study of carr development. Its position at the junction of Drainer's Dyke and Wicken Lode can be seen from Fig. 2. It consisted of a large central clump of old *R. catharticus* bushes, a scattered fringe of mature bushes of various species, and a central portion of well-grown mixed sedge, already in 1923 uncut for several years and showing rapid invasion by seedling bushes. In 1924 the area was enclosed by a wire fence (paid for by the generosity of Prof. A. G. Tansley), and it has been left to develop naturally, save for the disturbance of mapping, ever since. The first mapping was begun in the summer of 1923 and extended in 1924; the same ground was remapped in 1929 and again in 1934. As will be seen from the figures, only about two-thirds of the enclosed area was mapped. Here, as with the mapping technique, it was necessary to make constant compromise between the desire to achieve accuracy on the one hand and the desire on the other not to waste over detail time required to examine and record major effects. The first step in the technique was the establishment of a permanent base-line: this was afterwards made the fence line too, and it carried therefore a number of carefully set out permanent posts from which each resurvey is begun. This is the line marked B, D, F, etc., on the maps. The standard mapping technique was to put out by optical square off-sets from this base-line at intervals of 10 ft. Surveying poles were set at 10 ft. intervals along these off-sets, and the 10 ft. squares thus indicated were enclosed by measuring tapes and plotted by eye, major accessory measurements being taken by marked 6 ft. wands. All bushes over 3 ft. tall and 1 ft. in diameter were mapped, but this must be taken at best as a very rough criterion. Bush outlines are shown in all cases, and a rough lettering system was used to indicate the prominent components of the herbaceous vegetation. The latter feature has not, however, been reproduced in the maps, though reference is sometimes made in the text to observations based upon these records.

(a) *Validity of the map records*

For a true picture of the work, it must be pointed out that a great deal of the mapping was done under severe technical difficulties, for example, in shoulder-high saw-edged sedge, or in carr so dense that kneeling or crawling were the only possible positions. With this in mind it is important to discuss the exact degree to which the records may be trusted and the limits beyond which they fail. We may make the following points:

(1) As in the transect B, it was not possible to indicate each bush separately; a circle may mean one bush or one shoot, but more likely means one homogeneous crown of living shoots of one species, whether one bush, part of one bush, or part of two or more similar bushes. Thus, arguing from one year's

map to another, bush outlines must be interpreted with caution—what is plotted in one way the first time may be plotted differently afterwards.

(2) Crown outlines are not very accurately drawn, especially in the earliest map; their general area may be trusted but not their shape.

(3) The smudging of field records probably caused wrong names to be given to a few bushes.

(4) Experience has shown that the off-sets made in different years coincide very closely. Especially near the base-line the 10 ft. squares will be quite exactly fixed. Even 80 ft. from the base-line it appears that they are seldom 1 ft. out either way. This is shown by checks on the boundary fence and by the coincidence of the outlines or trunks of old bushes.

It is gratifying to note that the field notes written on the later maps often indicate features such as dead *Cladium* or dead sallows in the exact positions suggested by the change in bush outlines from those of earlier maps.

(5) It is probable that the 1923–4 map is considerably less accurate than the later maps.

It is realised that the maps show frequent errors, but it is believed that despite this they also show many major features of ecological interest which can quite safely be accepted within the limitations of technique outlined above. These features can best be discussed by considering first the general features of the maps of the whole area and then the detailed characters of five separate areas, each 30 ft. square, selected as specially instructive from various parts of the mapped area.

#### (b) General comparison of maps of the whole area

Two complete maps are reproduced: those of 1923–4 and of 1934 (Figs. 6 and 7). It should be noted that overlap of bush crowns is not shown where *R. catharticus* is involved, since the shape of this bush is here given in solid black. Particulars of overlap are shown in the detailed maps discussed later.

The 1923–4 map shows the size and shape of the major clumps of old bushes. In 1923 there was an open path round the largest clump; by 1934 the route will be seen to be entirely closed by bush growth. Especially note the growing up of the wide area to the south of this clump. Within the clump itself it is evident that *R. catharticus* has extended and *Salix cinerea* has diminished in amount. The details of this process emerge clearly from closer examination. The size of individual bushes has consistently increased. This is especially conspicuous with the *Viburnum* bushes.

Even in the earlier map there is a remarkable density of bush colonisation, again with a most marked preponderance of *Rhamnus frangula*. There is also a good deal of *Salix repens*, var. *fusca* typical of mixed sedge. In the 1934 map the creeping willow has not been killed out, but the development and con-



solidation of *Rhamnus frangula* bushes has proceeded to an astonishing degree. Large numbers of the bushes are now over 6 ft. tall and mapping them is exceedingly difficult. It seems clear that a comparatively short time will see dense young *R. frangula* carr over the area. As yet the sedge itself (*Cladium mariscus*) shows no signs of extinction in this part of the area.

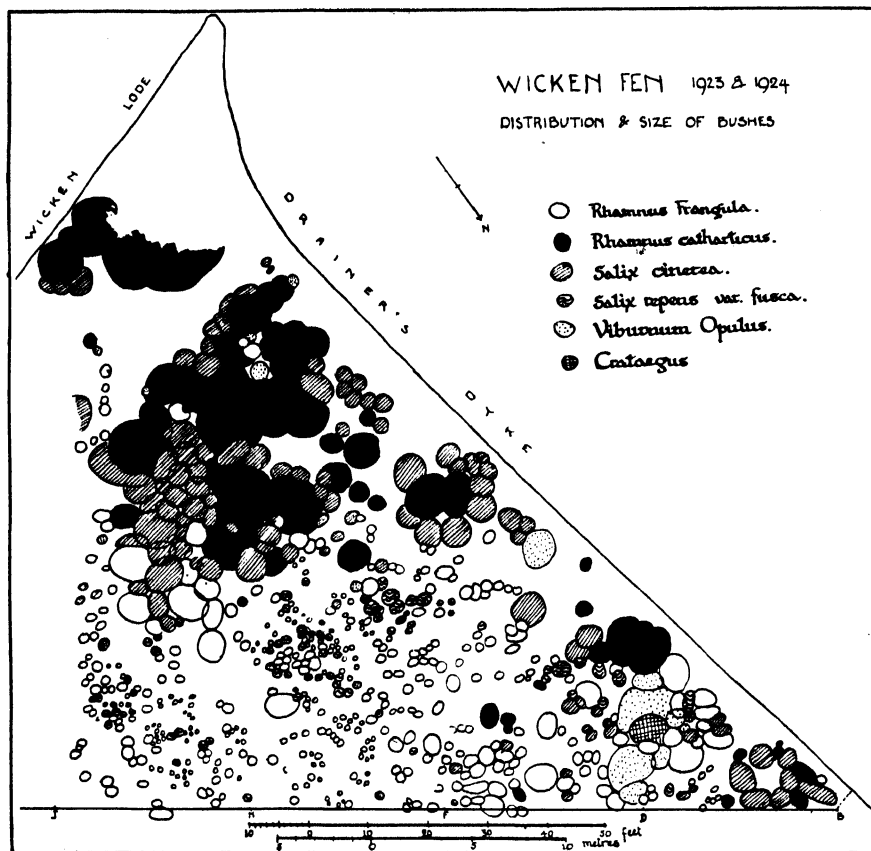


FIG. 6. Map of Reserve A, made in 1923 and 1924, showing outlines of crowns of all bushes over 1 m. tall and 50 cm. in diameter. In the central bush clump *Rhamnus catharticus* and *Salix cinerea* are the most frequent bushes, but in the area of open sedge to the north of this clump seedling *Rhamnus frangula* is very much the most abundant bush species.

It seems clear that the study of carr development must here concern three phases:

- (1) The lateral extension of established masses of carr over mixed sedge.
- (2) The internal processes of development within established masses of carr of different types.

(3) The colonisation of mixed sedge by seedling establishment and the development of these seedling bushes to form carr.

These phases will be recognised in the following detailed studies of the area.

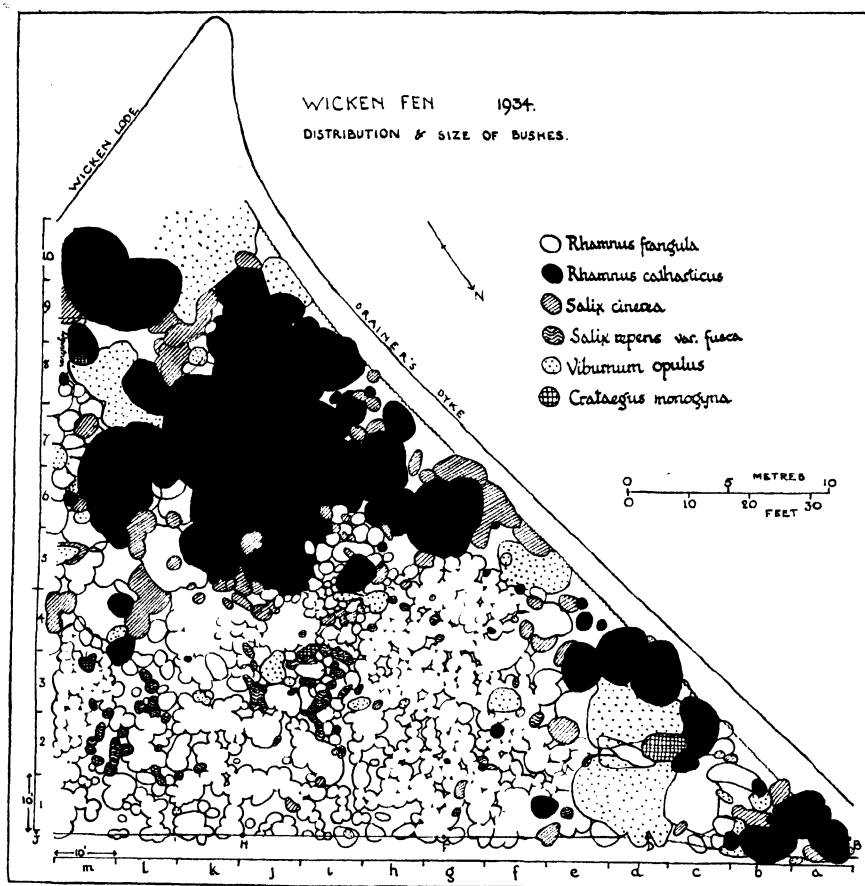


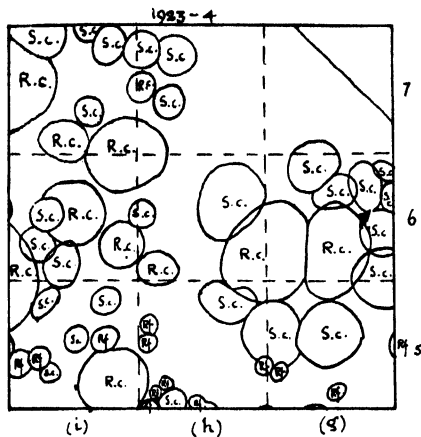
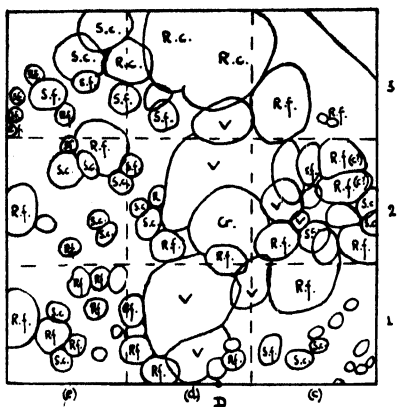
FIG. 7. Map of Reserve A, made in 1934, showing the outlines of crowns of all bushes over 1 m. wide and 50 cm. in diameter. In comparison with Fig. 6, there will be seen the rapid progress of bush establishment in the uncut sedge and the internal development of the central bush clump in which *Rhamnus catharticus* has become increasingly dominant and from which *Salix cinerea* has been extensively killed out.

(c) Squares c-d-e, 1-2-3 (Fig. 8)

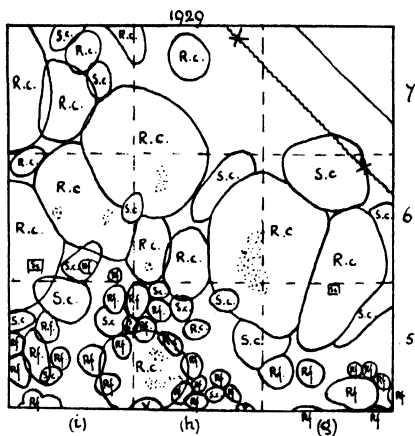
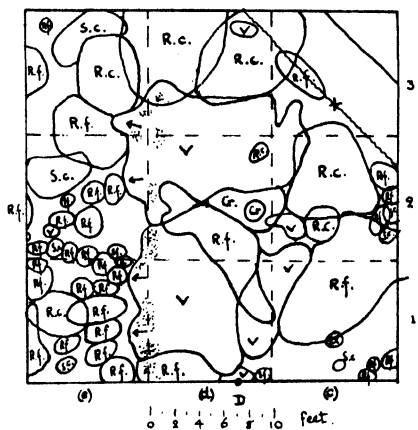
The position of these squares can be found by referring to the general map of Fig. 7; they lie on the base-line and close to the angle between this and Drainer's Dyke, and included in 1923 a clump of mature bushes and a wide belt of mixed sedge thickly scattered through with young bushes.

The most striking change shown is the enormous lateral spread of the old *Viburnum opulus* bushes, particularly over the sedge to the east. Between 1923 and 1929 they had

1923-4



1929



1934

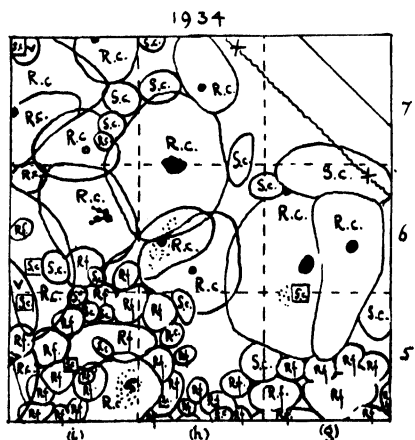
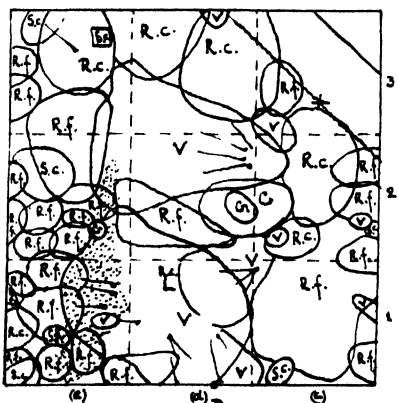


FIG. 8.

FIG. 9.

extended 5 ft. in this direction (they lie so close to the base-line that mapping error is excluded). The yearly extension of the twigs was found not to exceed 6 in., so that in all probability much of the extension is due to the falling over outwards of branches formerly erect. This is the impression given by the appearance of the bush. The bending over is due no doubt to the lateral development forced on the bush shoots by pressure of growth of other bushes in the centre of the clump, operating through the weight of wood, leaves and berries produced. It has been observed that branches so forced over into sedge may touch the ground, root and send up new vertical shoots, thus effectively colonising the sedge margin. An explanation of this kind is responsible for the "banyan habit" of *Viburnum*, which is most strikingly shown in various areas of mature carr in different parts of the Fen. A single bush may have a diameter of 50 ft., or have produced three successive generations of trunks, which, at first upright, have bent outwards, rooted and produced new trunks: the resulting growth is an impenetrable tangle below which the ground is bare. The great lateral extension of *Viburnum* between 1923 and 1934 is over ground occupied by living *Cladium* at the earlier date, and it will be seen in the maps both of 1929 and 1934 that beneath the fringe of advancing *Viburnum* close dotting shows the presence of dead *Cladium* plants. The radiating lines tapering out from a black dot in *c* 1 and *d* 2 represent the slope of major trunks of *Viburnum* from the stools, and they reflect the bending over processes we have just considered. The same effect is seen in *e* 1 upon the trunks of young *Rhamnus frangula* bushes pushed over by the advancing *Viburnum* bush: improbable as it might at first seem, the crowns of these *Rhamnus frangula* bushes have shifted several feet sideways since they were first mapped.

It will be noticed that other bushes than the *Viburnum* have extended greatly in crown area, notably the *Rhamnus catharticus* in *e* 3 and *d* 3, and the *R. frangula* in *c* 1. These bushes do not, however, fall over to the same extent as *Viburnum* and never reach the ground and take root again. It will be noted that extension of crown area is rapid on the open side of the bush clump and negligible on the inside of the clump: bushes do not extend and interlace their crowns with one another (note the *Rhamnus frangula* in *c* 1). It will also be seen that whilst lateral expansion is rapid before the bush crowns are in contact, for example, the *R. catharticus* bushes of *d* 3 between 1923 and 1929, after contact is made the extension almost ceases, as is shown by the same bushes between 1929 and 1934 after they have reached the crown of the *Viburnum* bush. The earlier phase of extension almost certainly involves a fanning out or "bending over" of the major trunks and branches of the bushes from one another.

It is interesting to notice the history of the small *Rhamnus catharticus* bush on the boundary of *d* 3 and *e* 3 in 1923; though it grew considerably its crown was pushed out to the east by growth of the main clump of older trees in later years. Itself it caused a *Salix cinerea* bush to bend farther eastwards, as is shown by the trunk line of the willow bush in *e* 3, 1934. Not only this but by 1934 a stool of *Salix cinerea* had died below the *Rhamnus catharticus* bush and its remains have been indicated by *Salix cinerea* in a square. Very often the pushing over of smaller bushes by larger ones is only a prelude to killing out of the former.

The crown expansion of *Rhamnus frangula* bushes has nothing like so severe a reaction upon the undergrowth as that of *Viburnum*. Below the extended crown of *Rhamnus fran-*

FIG. 8. Map of an area 30 ft. square inside Reserve A, mapped at three different times. During the period shown there has been a striking advance of the large *Viburnum opulus* bushes outwards from the main bush clump. Sedge (*Cladium mariscus*) killed out by this advance is shown by stippling.

FIG. 9. Map of an area 30 ft. square inside Reserve A, mapped at three different times. Note the increased number of bushes in the later maps and the much increased crown area of the larger bushes.

*gula* in c 1 the *Cladium* and *Phragmites* were still flourishing in 1934, though the *Arrhenatherum avenaceum* present in 1923 had gone.

The field notes also give another fact of interest, namely, that in d 2, under the shade of the old *Viburnum* bush, new sucker shoots of *Viburnum* are arising; these are weak and straggling and bend over and root readily. They make for a very complex bush structure almost or quite impassable by man.

Of the direct bush colonisation into the sedge one need only remark that by 1934 the coalescence of bush outlines has become nearly complete, though *Cladium*, and the dwarf willow, still persist in it.

(d) Squares g-h-i, 5-6-7 (Fig. 9)

These squares lie also on the Drainer's Dyke border of Reserve A, and in 1923 contained a few medium-sized bushes, not forming clumps, separated by mixed sedge.

The most marked feature of the change with time is the greatly increased spread of the *Rhamnus catharticus* bushes from 6 to 10 ft. or 7 to 11 ft. in the six years between 1923 and 1929. Thus in 1929 the crowns of these bushes have met, forming a continuous clump of *R. catharticus* reaching right across the width of three squares. Accompanying this there has been killing out of *Cladium* as shown by dotting in the figures.

The original mapping may have been at fault in the mapping of *Salix cinerea* bushes. Even bearing this in mind, however, the dead remains of sallow shown in the 1934 map leave little doubt that several bushes of this species present in 1923 have died by 1934, some, judging from their position, as a result of competition from taller *Rhamnus catharticus* bushes.

For the rest, one can only call attention to the rapidity of direct bush colonisation into the open sedge between 1923 and 1934; some of the bushes are recognisable from the earlier map and some are not.

(e) Squares i-j-k, 6-7-8 (Fig. 10)

This area, which also borders Drainer's Dyke, partly overlaps that last considered; it extends, however, sufficiently far to include a large part of the central clump of old *R. catharticus* bushes already referred to, and the changes in it are of particular interest. The positions of the chief bushes and of the enclave on the boundary of j 6-7 show the mapping off-sets to have been correctly laid out.

In the 1929 map there are fifteen dead bushes of *Salix cinerea* shown and many, e.g. in k 6 and 7, can be recognised as bushes which were living in 1923-4. This death is due to the eastwards spread of two large *Rhamnus catharticus* bushes. The *R. catharticus* has everywhere spread extensively, and locally shows dead *Cladium* beneath it.

Already in 1923-4 the bush growth had almost enclosed a sedge area at the junction of squares j 6 and 7, and i 6 and 7. This was then about 50 sq. ft., by 1929 it had shrunk to 8 sq. ft., and in 1934 it had completely disappeared in face of lateral expansion of surrounding adult bushes. The sallows which bordered the enclave have disappeared and some remains

FIG. 10. Map of an area 30 ft. square inside Reserve A, mapped at three different times. Bushes of *Salix cinerea* marked as living in the earliest map have disappeared in the later maps except for the small squares which indicate dead remains still recognisable. Note also encroachment upon and elimination of a small enclave of sedge by surrounding bushes and extension of *Viburnum* (creeping form below tall *Rhamnus catharticus*) in the latest map.

FIG. 11. Map of an area 30 ft. square inside Reserve A, mapped at three different times. It shows the rapid outwards extension of bushes on the margin of a large bush clump: the tapering lines show the bush trunks pushed over by the lateral movement of the crowns. The pushing over and killing of *Salix cinerea* is well shown, and also killing out of *Cladium mariscus* under carr of young *Rhamnus frangula* (cf. Pl. IV, Phot. 1).

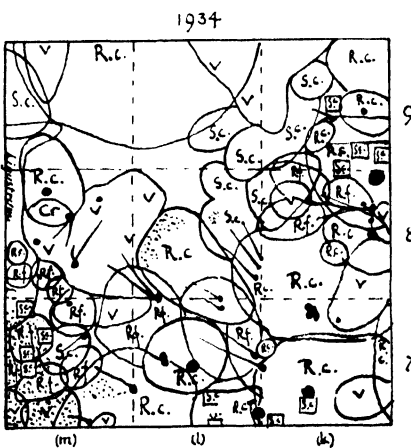
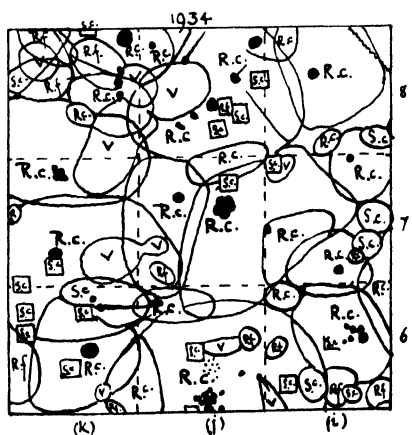
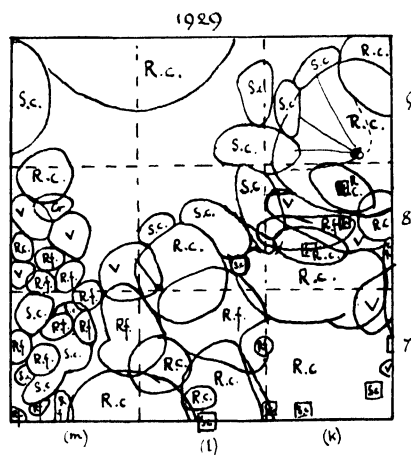
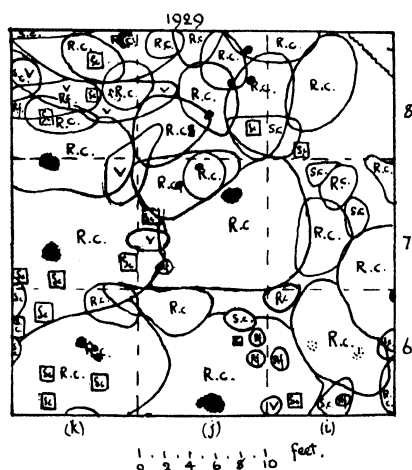
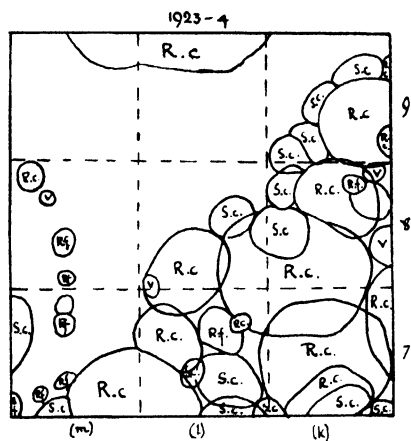
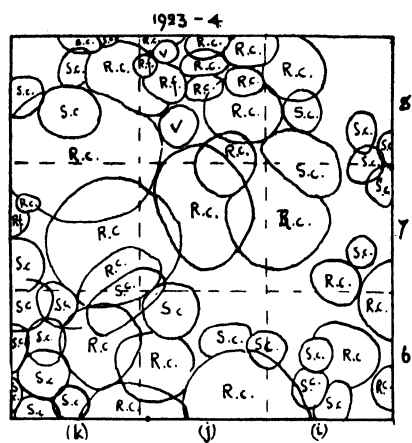


FIG. 10.

FIG. 11.

of them are shown in the 1934 map. In 1923-4 the enclave vegetation included *Dryopteris thelypteris*, *Ulmaria palustris*, *Molinia coerulea*, *Phragmites communis* and *Cladium mariscus*; by 1929 only *Ulmaria* and *Phragmites* persisted in the open enclave. The vegetation below the bush canopy in 1934 in the same place shows residual *Dryopteris*, *Ulmaria* and *Phragmites* plus *Agrostis alba*, though the tree canopy is not yet dense and the undergrowth is still quite abundant.

It will be seen that there are small bushes of different species below the shade of the tall *Rhamnus catharticus* bushes, and their different behaviour is of interest. The small *R. frangula* bushes shown in *i* and *j* 6, 1929, have been caught up by the lateral spread of the large *R. catharticus* bush, and in 1929 they are reported as "drawn up very tall and with no lower leaves or branches". Not so young *R. catharticus* in similar positions; this species branches and produces leaves freely in the shade. There is also evident from each map to the next considerable extension of *Viburnum opulus*, and this is due, especially in *k* 7 and 8, *i* 8 and *j* 6, to weak suckers of this species arising, drooping over, rooting and resuckering in the manner described above. Already a straggling tangle of some size has been produced, and its future will be a matter of considerable theoretical interest as it may well affect the future structure of the carr. It is not clear whether such *Viburnum* can arise directly from seed, but this is probable for the bush in the centre of *j* 6 (1934), and healthy seedling *Viburnum* is certainly quite often found on the floor of carr in the fen.

(f) Squares *k-l-m*, 7-8-9 (Fig. 11)

Running diagonally across this area is the south-east fringe of the central clump of tall bushes.

The detached bushes to the south of the clumps *l* 9 and *m* 9 were only roughly drawn in the first survey, but nevertheless the gap between them and the main clump has evidently narrowed greatly by 1929 and has quite closed up by 1934, leaving a comparatively small enclave. We can make out by examination some of the factors in this process. From 1923-4 to 1929 the margin of the main clump has moved 3-5 ft. outwards. The extension of the crowns of the tall *Rhamnus catharticus* has thrust over the fringing belt of willows, and the 1929 map shows their prostrate trunks originating well inside the area of the *R. catharticus* bushes (*k* 9). Between 1929 and 1934 at this point the advance of the clump was met by the advance of *Viburnum* and *Rhamnus catharticus* from the opposite direction and was held up. In *l* 8, however, the advance has continued, and here again is shown the pushing over of marginal willows and the bending of marginal *R. frangula* and *R. catharticus* (note the line of the trunks and position of stool and crown). Below the advancing margin of willow and *R. catharticus* are abundant remains of dead *Cladium*.

In *m* 8 it is worth noting the increase in size of the one *Rhamnus catharticus* bush shown in 1923-4, and the far greater rate of extension of *Viburnum*, this also pushed over by pressure of the developing clump, but unlike the other species rooting and suckering again from the prostrate shoots to form a dense tangle. Square *m* 8, 1934, also shows considerable extension of *Ligustrum vulgare*, a bush not common in the carr at Wicken.

Square *m* 7 and the adjacent part of *m* 8 show a very remarkable rapidity of bush development following seedling establishment. *Viburnum*, *Rhamnus frangula* and *Salix cinerea* are the bushes involved. By 1929 the bushes had begun to coalesce and by 1934 *Cladium mariscus* had been heavily killed out. Moreover, bushes of *Salix cinerea*, alive in 1929, are evidently represented by dead trunks in the map of 1934, clearly a result of the severe competition. The pioneer character of the willow in fen carr is emphasised by evidence of killing out in two other parts of this area, i.e. in *k* 9 (1934), where there are dead remains of some of the bushes pushed over by the marginal advance of the bush clump, and in *l* 7 and *k* 7 (1929), where dead willow bushes in the centre of the clump are shown in place of living bushes in the 1924 map. The same early death of the willow in competition with other

fen bush or tree species, its pioneer status and marginal position have been recognised in other fens, e.g. the Norfolk Broads (Godwin and Turner, 1933) and north-east Ireland (White, 1932).

(g) *Squares j-k-l, 4-5-6* (Fig. 12)

This area covers a part of the main bush clump containing a great deal of *Salix cinerea* in 1923-4, and a small portion of open sedge vegetation (*j 4*). Parts of it have already been considered in other areas.

Its chief interest is the progressive killing out of *S. cinerea* indicated by abundant dead remains in the maps of 1929 and 1934. It is also represented in the 1934 map by hatching in *l 5* and *6*, where, though the willow bushes are not quite dead, all the lower branches have been killed. The killing out of the willow is produced here by competition not only of *Rhamnus catharticus* but also of *R. frangula*.

The sedge vegetation in *j 4* shows bush colonisation and the development of young *R. frangula* carr to a stage of continuous canopy and killing out of *Cladium* in 1934.

#### V. TRANSECT C (INTERNAL DEVELOPMENT OF CARR)

Interesting as are the results from Reserve A, they do not illustrate all the major phases of carr formation. They show the early phases of establishment of young *Rhamnus frangula* carr, of the development of young mixed carr, and of the lateral extension of what may be regarded as fragments of mature carr dominated by *R. catharticus*. They illustrate also some features of the behaviour to be expected in carr containing *Viburnum opulus*, but as yet they give

FIG. 12. Map of an area 30 ft. square inside Reserve A, mapped at three different times. It shows progressive enlargement of crowns of established *Rhamnus catharticus* bushes, elimination of *Salix cinerea* from the developing carr (shown both by small squares representing dead stools and by hatching), and rapid establishment of young *Franguletum* in open sedge

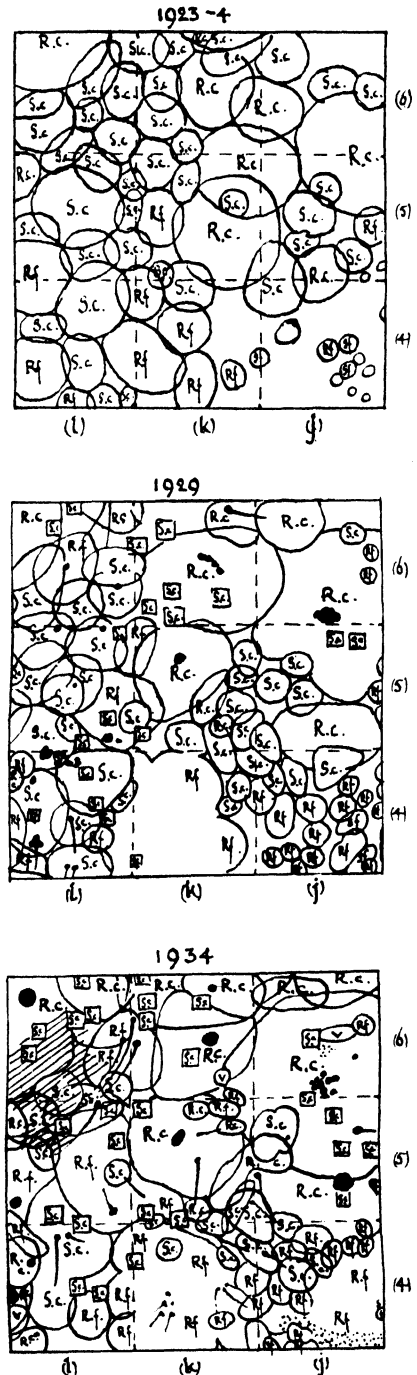


FIG. 12.



no indication of the later development of carr dominated by *Rhamnus frangula*. This is by far the commonest type of carr on Wicken Fen, and we have already suggested that this eventually develops into mature carr dominated by *R. catharticus*. In order to demonstrate, if possible, the fact and the manner of this replacement of one species by the other in mature carr, a belt transect 2 m. wide and 14 m. long was permanently set out in 1929 (Transect C, see Fig. 2). It actually lay within an extensive area of carr dominated by tall *R. frangula* but within 2 or 3 m. of older carr dominated by tall *R. catharticus* bushes. At this time it showed a number of dead and dying *R. frangula* bushes and contained a few small bushes of *R. catharticus*. It was very carefully surveyed by K. Saw of Downing College, Cambridge, who devoted several days to the task and mapped the outline of each bush crown, measuring its height above ground-level at different places. He also marked the position and height of dead trunks and identified them. The remapping was carried out by myself in 1934. The results of the two surveys are given in Figs. 13 and 14; the one giving plans of the area and the other *diagrammatic* profiles reconstructed from the map data of outline, height, etc. In the profile the canopy outline indicates no more than the rough height limits of the bush, and the trunks are naturalistic only in respect of number and site of the stools: similarly the dead stems show only height and rooting position accurately. To these qualifications it should be added that as in the other mapped areas it proved very difficult to define and map the contour of a bush, especially a bush of such diffuse form as *R. frangula*. The crowns, moreover, are liable to be moved from year to year by "pressure" of neighbouring bushes or by removal of "pressure" and gap formation where other bushes have died. All these factors are probably involved in the great differences apparent between the bush outlines of the *R. frangula* and *Salix cinerea* bushes in the 1929 and 1934 maps. The outlines of the *Rhamnus catharticus* bushes remain by comparison recognisably the same, though much enlarged, between one mapping and the next.

The results of the remapping may be summarised as follows:

*R. frangula* bushes have shown considerable mortality; the lowest of the three transects in Fig. 13 shows all the dead bush stumps present in 1934. These are very numerous and consist almost entirely of *R. frangula*. Twenty-five of these dead stools are unmarked in the 1929 mapping, but only ten of these can be safely identified as having been alive in 1934. Others of the dead stools of 1934 occur in positions still covered by a canopy of living *R. frangula*, below which the living stools probably were not all mapped in 1929. Examination of the two profile diagrams (Fig. 14) will show the dead *R. frangula* bushes to have been among the *tallest* bushes in the transect: thus at the west end of 1929 transect there are five *R. frangula* bushes which reach 3 m. or more in height, and of these four are dead in the 1934 transect. At 6-7 m. two other very tall bushes of *R. frangula* have died.

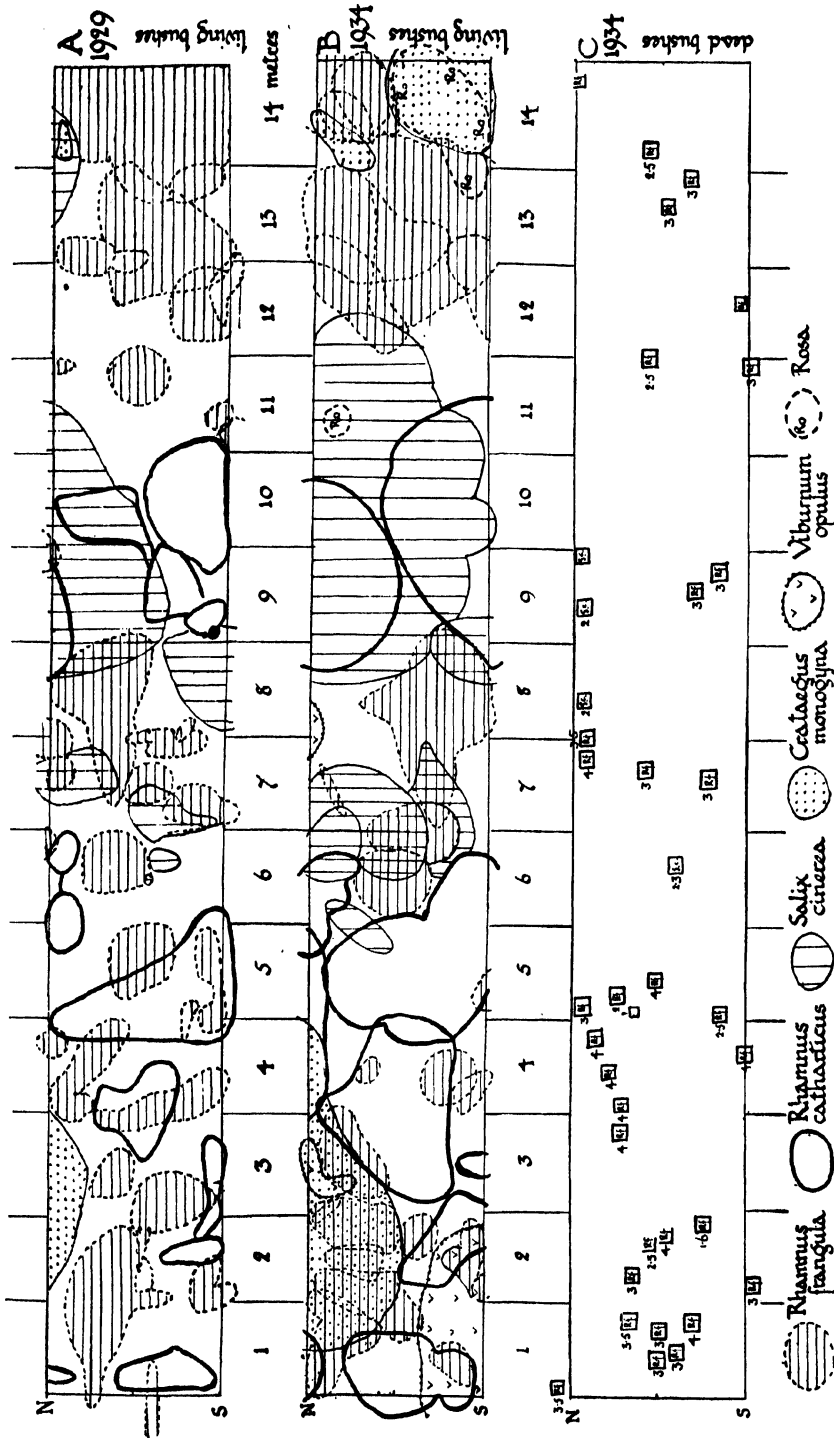


FIG. 13. Map of bush distribution in belt Transect C situated in the ecotones between developing Franguletum and carr dominated by *Rhamnus catharticus*. Map A shows the bush outlines in 1929, Map B the outlines in 1934, and Map C the position of all the dead stools present in 1934, with their heights in metres. Bushes of *R. catharticus* have changed little in position between 1929 and 1934, but have enlarged considerably. There are large differences during this time both in position and extent of the *R. frangula* bushes.

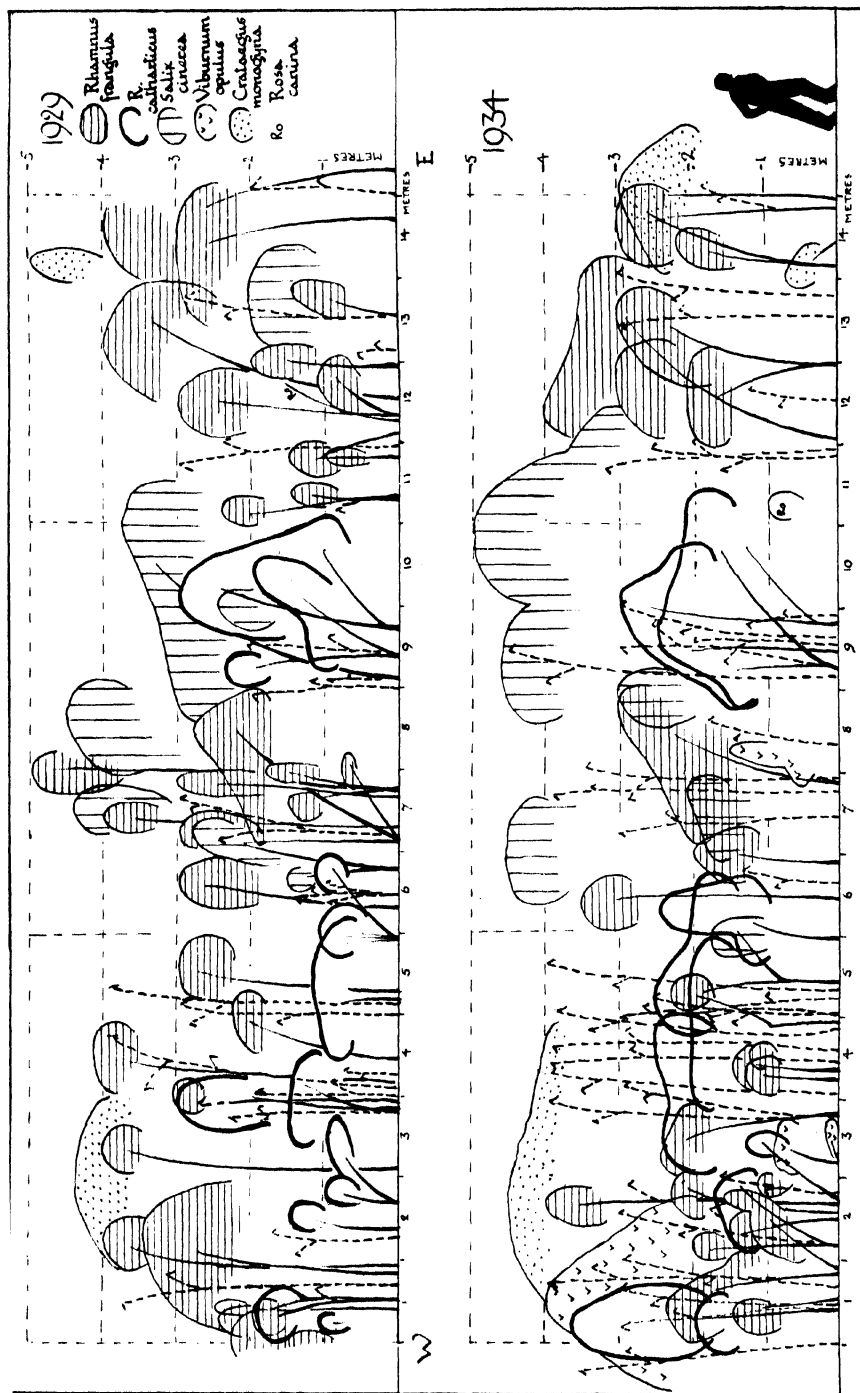


FIG. 14. Diagrammatic profiles of Transect C reconstructed from the maps and field notes of the height of bushes. The trunks are shown symbolically, but indicate correctly the observed height and rooting position. Many tall bush crowns of *Rhamnus frangula* present in the 1929 profile are absent from the 1934 profile, and these may in some cases be identified with dead trunks (upright broken lines) shown in the later profile. All the *R. cathartica* bushes present in 1929 are still alive in 1934, but are much taller.

The dying *R. frangula* which remain in the 1934 transect are also tall. Thus death is unlikely to be an effect of shade competition from other bushes, a suggestion supported by the fact that the lower part (0.5–1.0 m.) of such bushes may be still alive and producing sucker shoots though the top has died. K. Saw, after mapping the transect in 1929, wrote to the same effect. "If a future map of the same transect shows that *R. frangula* has nearly all died out and *R. catharticus* has become dominant, it will not prove that shading is the important factor, even though it may seem to be so now. That such an inference would not be a just one is evident from the fact that many of the dead shoots are higher than the surrounding competitors."

After the death of *R. frangula* bushes the growth of basal shoots and the extension of the remaining healthy bushes produce a canopy almost as dense as before, but the number of stools is fewer and the height of the crowns less.

It does appear from the transect maps that *R. frangula* is rapidly diminishing in this area of carr: it will be shown in the next section of the paper that this effect is probably due to severe and widespread fungal attack.

In contrast with *R. frangula*, none of the *R. catharticus* bushes has died between 1929 and 1934. New bushes have not appeared but the old bushes have increased much both in height and diameter of crown; the individual bushes are recognisable in both maps.

*Viburnum opulus* does not appear at all in the figures for 1929, but since then the west end of the transect has become overhung by a large bush, and prostrate shoots of *Viburnum* have crept in at three places and in two are rooted in the transect.

*Crataegus monogyna* shows increase in the size of the bushes present in 1929. The absence of the large hawthorn bush in 13–15 m. from the map of 1929 must have been due to intentional omission at the end of the transect.

A diminution is shown in the numbers of *Salix cinerea*. Three of the dead *S. cinerea* stools in the 1934 diagram were living bushes in 1929, but the remainder have increased in height and spread. In view of what we have seen from the mapping of Reserve A of the readiness with which *S. cinerea* succumbs to the competition of other species, its survival here shows that the carr is now by no means dense, and confirms the view that the *Rhamnus frangula* is not being killed by shading out.

The processes indicated in this study of the changes of five years certainly seem to be such as would lead eventually to dominance by *R. catharticus* in place of *R. frangula*.

## VI. DIE-BACK OF *RHAMNUS FRANGULA* AND ITS ECOLOGICAL IMPORTANCE

About 1928 my attention was first caught by signs of very extensive dying out of tall *R. frangula* bushes in fairly mature carr in plot 608 on Wicken Fen. The dead bushes were conspicuous by the contrast made by the whitish yellow peelings from the bark of dead erect stems, and the carr undergrowth showed

rapid response by increased height and luxuriance to the lightening bush canopy. The appearance of carr showing extensive dying back of *R. frangula* bushes is seen in Pl. IV, phot. 2. Direct examination in the carr in summer showed several bushes with trunks evidently killed within the last day or two, since wilted but still green leaves were hanging abundantly on the crown. Bark stripping in all such cases revealed a very interesting aetiology. Always there was a strip of black coloration of wood and bark extending some feet along the trunk; traced downwards this led to a point where lateral extension had evidently just brought about complete ringing, no doubt the immediate cause of the wilting and of death. Traced upwards the blackening was found to originate in some snag formed round the base of a dead lateral shoot. Snags formed by the breaking of later branches are extremely frequent in *R. frangula*, and they are very frequently infected by fungi which cause, as in these cases, considerable local hypertrophy. It is, in fact, extremely difficult to find on the fen any mature *R. frangula* bush free from such cankers, but in young or isolated bushes the fungus appears to be localised and the bush recovers from the attack.

Samples of the recently killed branches were taken back to Cambridge, and from the junction between the infected and healthy wood at the point of ringing it proved possible to see fungal hyphae grow out of the fungus in culture. This work was carried out by G. C. Stevenson, who identified the fungus as a *Fusarium*. When Stevenson left England, Mr F. T. Brooks readily agreed that another of his research students should take up the problem and R. E. D. Baker carried out a general preliminary investigation on which he has reported as follows:

#### THE DIE-BACK OF *RHAMNUS FRANGULA* ON WICKEN FEN

By R. E. D. BAKER

##### *Introduction*

During 1930 an investigation into the cause of the die-back of *R. frangula* bushes on Wicken Fen was started by G. C. Stevenson. This was continued during 1931 and 1932.

Various fungi have been isolated from junctions between diseased and healthy tissues by plating out pieces of the wood on Dox's medium in Petri dishes. These fungi have been kept in culture on this medium and inoculated into bushes on the Fen. The inoculations were made as follows: A wound was made into the cambium of a branch between  $\frac{1}{2}$  and 1 in. in diameter, and a piece of mycelium was inserted into this and moistened with sterile water. The wound was then bound up with black wool, labelled, and left. Controls were made in an exactly similar fashion, omitting to put in the mycelium.

##### *The appearance of the disease on the Fen*

Many dead and dying bushes of *R. frangula* are to be found in the mature carr on the Fen at all times of the year. Also branches which have suddenly died back in the summer while the leaves were on have been found; these are the most valuable from which to make



Phot. 1. (G. E. Briggs.) Photograph taken in young carr dominated by *Rhamnus frangula*, showing the numerous trunks which arise from each stool. Although no living plants of *Cladium mariscus* are now present, its previous existence is shown by the large bunches of dead leaves caught up in crotches of the branches of *Rhamnus*.



Phot. 2. A view from a cleared area on the margin of a mature *Rhamnus frangula* carr. The very abundant die-back of the bushes is shown by the leafless branches from which the bark is peeling. The foreground shows abundant *Pragmites communis* and centrally a bush of *Salix cinerea*.



isolations. *Nectria cinnabarina*, of which more will be said later, is very common on the dead wood of many of these bushes.

#### *The fungi isolated*

In all six species have been isolated, including *Nectria*. These are (1) *Diplodina* sp. (2) *Cytosporina* sp., (3) *Phoma* sp., (4) *Diplodia* sp. (*Frangulae* ?), (5) *Fusarium* sp., (6) *Nectria cinnabarina*. Numbers (2), (3) and (4) proved to be saprophytic only, and caused no injury to the bushes when they were inoculated with them.

#### (1) *Diplodina* sp.

On Dox's medium. Mycelium white at first, greenish later; pycnidia black, spores uni-septate, hyaline, 22 by 10  $\mu$ .

In the inoculations this fungus produced a slow blackening of the bark and wood around the point of inoculation, but this never spread for more than 6 in., and the branch was not killed in six months. This fungus therefore could not be the primary cause of the die-back although it is undoubtedly parasitic on *Rhamnus frangula*. This fungus was twice successfully re-isolated from the inoculations.

#### (5) *Fusarium* sp.

Mycelium orange-red in culture. Macroconidia produced in sporodochia, yellow in mass but hyaline under the microscope. Microconidia produced in dense aggregations superficially resembling sclerotia, and also scattered all over the surface of the colony.

When inoculated into *Rhamnus frangula* this fungus produced a very rapid blackening of the wood and bark and killed branches an inch in diameter in six months. These were too far gone for successful re-isolations to be made, and only the saprophytic *Phoma* sp. was obtained. Earlier on, the *Fusarium* was successfully re-isolated when the blackening had only spread about 8 in. from the point of inoculation. The branch appeared to be killed by a rapid destruction of the bark, the wood being attacked more slowly.

#### (6) *Nectria cinnabarina*.

Cultures were made from material collected on the Fen and also from *Nectria* growing elsewhere on dead wood. These cultures were very similar, and the *Nectria* growing on the *Rhamnus frangula* on Wicken Fen appears to be *Nectria cinnabarina* or a form very closely allied to it. It is commonly found at the base of branches where it appears to behave as an active parasite, ringing the bark and killing the branch. It was especially common during the late summer and autumn of 1931. Both strains of *Nectria* were inoculated into *Rhamnus frangula*, where they both produced cankers and a blackening of the bark. They were successfully re-isolated.

#### *Conclusions*

There appears to be little doubt that both *Nectria cinnabarina* and the *Fusarium* sp. are concerned with the die-back of *Rhamnus frangula* on Wicken Fen. Both forms are successful wound parasites and would appear to enter either where twigs have been broken off, or where two branches have produced a lesion by rubbing together. Other saprophytic fungi follow rapidly in the wake of these two species.

#### *Ecological significance of the die-back*

These fungi definitely shorten the life of the *Rhamnus frangula* bushes and may explain why they are replaced by *R. catharticus* in the older carr on the Fen, as this species is apparently not attacked by the disease.

Dr Baker's investigations certainly establish the fungal character of the extensive die-back of *R. frangula* in the carr of Wicken Fen, and we have seen reason to connect this with the process of replacement of carr dominated by



*R. frangula* by carr dominated by *R. catharticus*. If these are the facts, we appear to be confronted with a case of widespread fungal attack as a major and regular factor in seral development, a phenomenon not, I think, previously recorded. It is, of course, possible that the die-back is due to other unsuspected factors with sporadic and local incidence, but it is more likely that the incidence of severe die-back always occurs in maturing carr, possibly encouraged by the conditions so produced, more likely merely by increasing age of the component bushes, most of which date from the period of seedling colonisation of open herbaceous communities.

The die-back which has been described is, however, by no means the only evidence of the incidence of fungal attack on the fen bushes. In early summer both *R. frangula* and *R. catharticus* show very abundantly over their leaves and twigs the bright orange aecidial clusters of the rust fungus, *Puccinia coronata*. This fungus and its host relationships on the Fen have been very closely investigated by Miss M. R. Brown, who has kindly prepared the following summarised account of the bearing of her work on the problems of bush colonisation.

#### THE INFECTION OF *RHAMNUS* SPECIES AT WICKEN FEN BY THE AECIDIAL STAGE OF *PUCCINIA CORONATA* CORDA

By M. R. BROWN

Both *Rhamnus frangula* and *R. catharticus* are commonly infected at Wicken by the aecidial stage of the crown rust, *Puccinia coronata* Corda, which has been found to have the alternate stage of its life cycle upon various of the Fen grasses.

During the summers of 1933 and 1934 the uredo- and teleutospore stages of the rust were recorded at the Fen on the following species of grass:

	Phalaris arundinacea	} Heavily infected.
	Calamagrostis lanceolata	
	C. epigeios	
	Lolium perenne	
	Festuca elatior	
	Holcus lanatus	
	Arrhenatherum avenaceum	
and	Agropyron repens	} Slightly infected.
	Agrostis palustris	

Inoculation experiments with teleutospores collected on these grasses confirmed the results obtained by Klebahn and Eriksson and showed that the biologic forms of this rust on *Phalaris arundinacea* and *Calamagrostis lanceolata* gave rise to aecidia on *Rhamnus frangula* but not on *R. catharticus*. On the other hand, the forms on *Lolium perenne*, *Festuca elatior*, *Holcus lanatus* and *Arrhenatherum avenaceum* produced aecidia on *Rhamnus catharticus* only. *Calamagrostis lanceolata* and *Phalaris arundinacea* are two of the most abundant grasses on the Fen and occur almost all over its area, while *Lolium perenne*, *Holcus lanatus*, *Festuca elatior* and *Arrhenatherum avenaceum* are confined to the droves and pathways. The two biologic forms which infect *Rhamnus frangula* are thus more abundant and more widely distributed over the Fen than those infecting *R. catharticus*.

The teleutospores of the rust begin to germinate at the end of April, and the first signs of aecidial infection appear about the second week in May, when spermogonia are observed on the leaves of the two *Rhamnus* species. Aecidia appear in 7–10 days and continue to be formed until the latter part of July. They arise on the leaves and young twigs, and the presence of the mycelium in the tissues causes considerable hypertrophy and distortion, particularly in the twigs. The infection is noticeably heavier on *R. frangula* than on *R. catharticus*, throughout the Fen. Considerably more infection spots occur on the leaves and the distortion of the twigs is more marked.

When the aecidia have ripened and shed their spores they shrivel and die and the host cells containing the mycelium are also killed. The infected leaves thus show dark brown islands of dead tissue corresponding to the areas on which the aecidia were borne. Where these infection spots are particularly numerous the whole leaf may shrivel and drop off. This defoliation is never severe on the Fen, and no cases have been known in which *Rhamnus* plants either adult or seedling have been killed by the fungus. One- and two-year-old seedlings of both species of *Rhamnus* were inoculated in the greenhouse and very heavily infected, but in no case was a plant killed. Some defoliation occurred and the young shoots were much distorted. Their growing points, however, remained uninjured and gave rise to new shoots which were quite normal and unaffected by the fungus.

It does not seem, therefore, that infection by *Puccinia coronata* causes any permanent harm to the *Rhamnus* plants, though the vigour of their growth must be reduced somewhat during the months of May and June. This reduction in vigour is probably greater in *R. frangula* than in *R. catharticus*, but it does not seem likely that this would be sufficient to influence the succession in favour of the latter.

It is to be hoped that other phytopathologists may be able to turn attention to a closer examination of the problems of fungal disease in the fen vegetation, especially those of such evident ecological importance as the die-back of mature *R. frangula*, the terminal die-back of the shoots of seedlings of the same plant (a very common phenomenon), and the die-back of mature *Salix cinerea*.

## VII. MECHANISM OF CARR DEVELOPMENT

Wicken Fen does not contain a sufficient number of examples of mature carr of different types to warrant their classification and description as specific vegetational types nor the construction of a successional scheme in which they are linked together. Nevertheless, the chief types of carr present may be very usefully employed as examples of the operation of the processes of vegetational development indicated earlier in the paper. The part played by chance in carr formation is considerable, both in respect of the initial density of bush colonisation and in the proportions of different species represented.

Some of the chief features of carr development are illustrated by the table set out on p. 114. This shows the hypothetical trend of development in two cases very frequently met with, dense initial colonisation of *Rhamnus frangula* bushes in mixed sedge, and much more open colonisation. If initial colonisation is dense the sedge vegetation is very rapidly killed out as the bush canopy closes, and is replaced by specialised shade vegetation. Thus when with increasing age the bushes show abundant die-back it is this shade vegetation which increases in luxuriance, and is maintained until the invading *R. cathar-*

*ticus* bushes dominate the carr. On the other hand, if initial colonisation is sparse the sedge vegetation persists relatively unaltered for a very long time. It will still be present in greater or less degree when the *R. frangula* bushes begin to die back, and will increase again in luxuriance as this causes further opening of the bush canopy. Locally the shade flora of denser bush clumps augments this vegetation, but it remains for a very long time substantially a sedge vegetation sown with living and dying bushes of various ages.

I. Dense initial *R. frangula* ecesis

Phase	Bush components	Factors in carr development	Ground vegetation
(a) Dense seedling colonisation into mixed sedge (c. 20 years)	Very largely <i>R. frangula</i>	Coalescence of crowns, filling-in enclaves: no seedling growth	Sedge components dying ( <i>Cladium</i> , <i>Phragmites</i> and <i>Salix repens</i> )
↓			
(b) Young <i>R. frangula</i> carr with dead <i>Cladium</i>	Elimination of <i>Salix cinerea</i>	Enlarging bush crowns. Internal competition	Much bare ground. Abundant <i>Dryopteris thelypteris</i> and persistent vegetative shoots <i>Lysimachia vulgaris</i> , <i>Symphytum vulgare</i>
↓			
(c) Mature <i>R. frangula</i> carr	Lessening <i>R. frangula</i> , establishment of <i>R. catharticus</i> seedlings	Die-back of <i>R. frangula</i> . Opening of canopy	Increase in vegetation present
↓			
(d) Transition carr	Increase in <i>R. catharticus</i>	Enlarging <i>R. catharticus</i> crowns and die-back of <i>R. frangula</i>	Lessening of ground vegetation. More bare ground. <i>Dryopteris thelypteris</i> , <i>Rubus caesius</i> , <i>Urtica dioica</i> , <i>Agrostis alba</i>
↓			
(e) <i>R. catharticus</i> carr	Dominance of <i>R. catharticus</i> ? entry of prostrate <i>Viburnum</i>	Lateral expansion of carr. Diminution of bush numbers. Single tree trunk form and high canopy	Increase in ground vegetation

II. Open initial *R. frangula* ecesis

(a) Open seedling colonisation into mixed sedge	Very largely <i>R. frangula</i>		Sedge components persisting
↓			
(b) Open <i>R. frangula</i> carr		Continued seedling growth. Local clumps showing internal competition	Sedge components living but drawn up. Abundant <i>Phragmites</i> , <i>Cladium</i> , <i>Salix repens</i> . Locally <i>Rubus</i> and <i>Dryopteris</i>
↓			
(c) Open <i>R. frangula</i> carr	Lessening of old <i>R. frangula</i>	Die-back of <i>R. frangula</i>	Increase in size and abundance of sedge components and <i>Rubus caesius</i>
↓			
(d) Denser <i>R. frangula</i> carr or mixed carr ?	? Increase in <i>R. frangula</i> and other species		

These two cases illustrate the great influence upon later development which the initial chance of dense or sparse colonisation may have. It will be recognised that there is in fact a continuous series between the two types we



Phot. 3. A fragment of mature carr containing bushes of *Rhamnus catharticus*; these are of tree form, having a single straight trunk unbranched below, arising from each stool, and a narrow crown. In the background are bushes of a much younger carr stage. The ground vegetation, which is influenced by the locally open canopy, includes *Eupatorium cannabinum*, *Iris pseudacorus*, *Rubus caesius* and *Urtica dioica*. The bush on the extreme left is *Crataegus monogyra*.



have discussed and that no considerable area is evenly sown with bushes, so that the carr at any stage is a mosaic of fragments of varying bush density. An additional complexity is added by the fact that other bushes such as *Crataegus monogyna*, *Viburnum opulus*, *Salix cinerea* and *Prunus spinosa* may form local clumps developing within the *Rhamnus frangula* carr and constituting centres of seed dispersal.

The table has intentionally omitted the later stages of bush colonisation, for very few of these are present on the Fen. Trees of various species, *Quercus robur*, *Fraxinus excelsior*, *Betula alba*, *B. pubescens*, and *Populus canescens* all colonise various fen communities, including carr. Former crop-taking on the fen and paucity of seed parents, however, prevent tree invasion from being anything more than extremely sporadic. Thus, though analogy with mature carr development in the Norfolk Broads and elsewhere suggests that deciduous woodland is the normal climax of these fen successions, no evidence is yet available as to its nature in Wicken Fen. The absence of natural alder (*Alnus glutinosa*) from Wicken Fen is a feature of striking difference from the carr of the Norfolk Broads, especially since alder pollen and wood is abundant through the full depth of the Fen peat. A few planted alders produce abundant viable seed, but no seedling establishment occurs.

#### SUMMARY

The processes of bush establishment in Molinieta and Cladio-molinieta on Wicken Fen are discussed in the light of changes in a permanent belt transect mapped in 1923, 1927, 1931 and 1935, and of numerical analyses of cleared areas of young carr. The most important colonising bush species are *Rhamnus frangula*, *R. catharticus*, *Salix cinerea* and *Viburnum opulus*, of which the first named is by far the most abundant.

An experimental and observational analysis of the factors responsible for the preponderance of seedling *Rhamnus frangula* over *R. catharticus* suggests that it is not concerned with differential seed production, germination or effects of soil acidity. The drupes of both species are freely dispersed by birds, but large numbers fall directly to the ground: the stones of both species are eaten by field mice which may in some cases also be dispersal agents, but no differential effect in dispersal seems to be responsible for the great relative abundance of *R. frangula* seedlings. This is at present attributable to the very great preponderance of *R. frangula* seed parents, but there is no evidence to show how this condition itself arose.

Early stages of carr (scrub) development are recorded in mappings made in 1923-4, 1929 and 1934 of a reserved uncut area of fen. There is clear evidence of the very rapid extension of bush crowns, especially of *R. catharticus*, with a corresponding killing out of *Salix cinerea*. *Viburnum opulus* especially expands by fanning outwards of the main trunks, which bend over and may take

root where they reach the ground and produce new erect shoots. It expands similarly when young shoots become prostrate below the shade of larger bushes.

Later stages of development of *Rhamnus frangula* carr have been investigated by permanent transect in the zone of transition to older *R. catharticus* carr, and some evidence is given to show that *R. frangula* may eventually all die out and be replaced by carr dominated by *R. catharticus*. The cause of this displacement seems not to be a direct effect of competition but of widespread fungal die-back of mature bushes of *R. frangula*. Specific isolation and inoculation experiments indicate that *Nectria cinnabarina* and a *Fusarium* species are the fungi responsible for this important seral change.

Finally a scheme is developed to show the very great influence upon carr development which the initial chance of dense or sparse colonisation may have.

#### REFERENCES

- Godwin, H. "Studies in the ecology of Wicken Fen. I. The ground water level of the Fen." *This JOURN.* **19**, 1931.
- Godwin, H. and Bharucha, F. R. "Studies in the ecology of Wicken Fen. II. The Fen water table and its control of plant communities." *This JOURN.* **20**, 1932.
- Godwin, H., Mobbs, R. H. and Bharucha, F. R. "Soil factors in Wicken Sedge Fen." *The Natural History of Wicken Fen*, Part VI, 1932.
- Godwin, H. and Tansley, A. G. "The vegetation of Wicken Fen." *The Natural History of Wicken Fen*, Part V, Cambridge, 1929.
- Godwin, H. and Turner, J. S. "Soil acidity in relation to vegetational succession in Calthorpe Broad, Norfolk." *This JOURN.* **21**, 1933.
- White, J. M. "The fens of North Armagh." *Proc. R. Irish Acad.* **40**, B, 15, 1932.
- Woodruffe-Peacock, E. A. "A fox-covert study." *This JOURN.* **6**, 1918.

# STUDIES IN THE ECOLOGY OF BRECKLAND

## I. CLIMATE, SOIL AND VEGETATION

By A. S. WATT

*(With 1 Map and six Figures in the Text)*

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### POSITION AND TOPOGRAPHY

BRECKLAND is a well-defined physiognomic unit whose vegetational features are primarily determined by a dry soil in a dry climate.

Breckland (Fig. 1) rests on a foundation of chalk and lies in south-west Norfolk and north-west Suffolk at the angle made by the chalk outcrop as it swings round from a south-west-north-east to a south-north direction. Here the chalk strata are practically horizontal and there is no escarpment. "The Cretaceous escarpment running south from Hunstanton is interrupted near Swaffham by a gap about twenty-five miles (40 km.) in width, which extends from that place to a point north-east of Newmarket, where the Chalk Hills of the Gog-Magogs commence" (Harmer, 1910). Opposite the gap lies Breckland. Set back from the line of the Lower Greensand and Gault outcrops, Breckland's western boundary is formed by the Fen, which here has extended eastwards partly at least at Breckland's expense. To the north and north-east, and south and south-east lies higher ground (61 m. to over 122 m.), separated by the trough of the joint basin of the west-flowing Little Ouse and the east-flowing Waveney: "possibly of pre-glacial origin, it was clearly in existence in glacial times" (Harmer, 1910).



The surface of Breckland is undulating with gentle slopes, rolling Down country without the steep-sided coombes. Three rivers rising in the higher

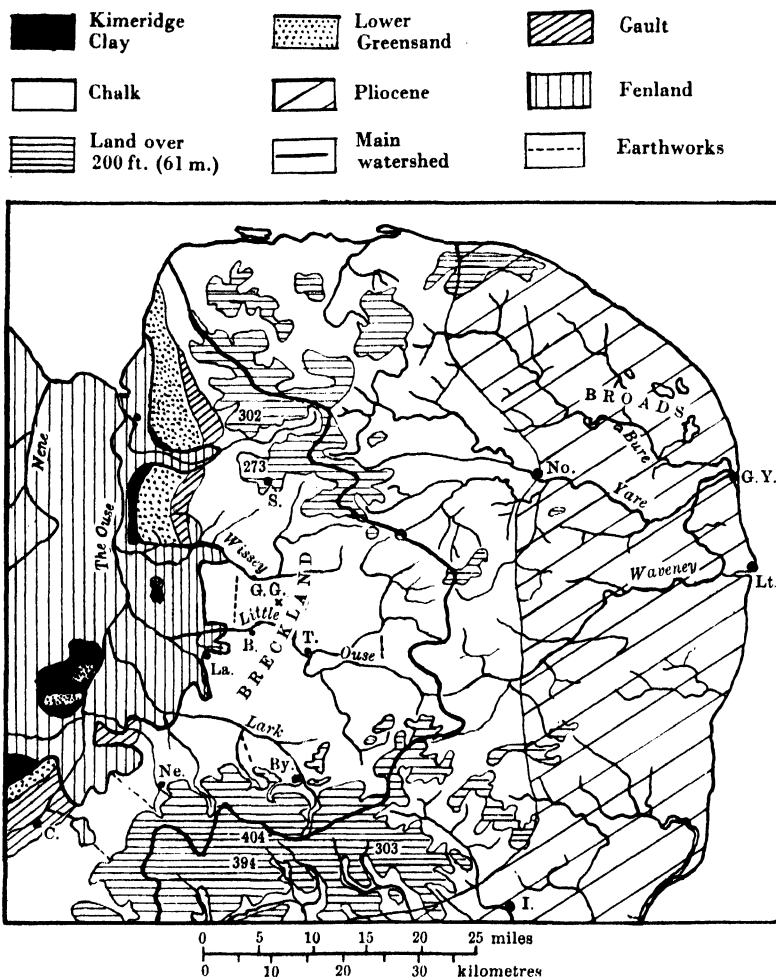


FIG. 1. Map of East Anglia to show the position of Breckland in relation to the solid geology and topography. It will be noted that the higher ground is nearly all on the chalk outcrop which runs through East Anglia in a broad belt from north to south. Breckland occupies the central lower ground between the higher ground to the north and south. The positions of some of the more important places are indicated by capital letters: B.=Brandon, By.=Bury St Edmunds, C.=Cambridge, G.G.=Grimes Graves, G.Y.=Great Yarmouth, I.=Ipswich, La.=Lakenheath, Lt.=Lowestoft, Ne.=Newmarket, No.=Norwich, S.=Swaffham, T.=Thetford.

ground to the north, east and south, flow westwards along a gentle gradient into the Fen: the Wissey near the northern boundary, the Lark near the southern, and the Little Ouse cutting Breckland into two approximately equal halves. The absence of tributaries is noteworthy, although there may be

considerable accession to the streams from underground drainage. Along the basins of these rivers long fingers of fen stretch into Breckland.

The northern half of Breckland rises gently from the Fen; the bulk of it lies between 15 and 45 m. above sea-level, small areas only in the eastern part rising above 45 m. to a maximum of 56.4 m. In its eastern part lie the meres at an altitude of about 32 m. and a little over.

Fronting the Fen, in the southern half of Breckland, is a line of gravel-capped hills rising to over 30 m. They are separated by low ground over which the Fen or transitional Fen has advanced up to a height of approximately 6 m. Thereafter the ground rises gently, then more steeply, to a relatively elevated plateau, a quarter or more of which lies above 45 m. with a maximum of 58.2 m.

The higher ground to the north-east gives Breckland little or no protection from the keen north-east winds, but its inland setting and its remoteness from the Atlantic appreciably influence its general climate.

### CLIMATE

A comparison of the meteorological data<sup>1</sup> for Valencia (south-west Ireland), Cambridge (32 km. south-west of Breckland) and Berlin—all approximately at the same latitude—brings out the departure from oceanicity and the approach to continentality shown by the hinterland of East Anglia.

### *Temperature*

In the mean annual temperature, in the range of temperature throughout the year, in the summer maximum (in July at Berlin and Cambridge: in August at Valencia) and winter minimum, Cambridge occupies an intermediate position (Table I, and Fig. 2).

Table I. *Temperature data for Valencia, Cambridge and Berlin: the mean annual, the mean monthly (for East Anglia as well) and the monthly extremes in °C.*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Mean annual tem- perature
Monthly means:													
Valencia	6.9	6.9	7.2	9.0	11.2	13.7	14.9	15.0	13.7	10.9	8.5	7.5	10.45
Cambridge	3.1	3.9	5.4	8.2	11.6	14.7	16.6	16.2	13.9	9.7	6.2	3.9	9.45
Berlin	-0.7	0.5	3.2	7.6	13.2	16.7	18.0	17.0	13.8	8.8	3.8	0.7	8.55
East Anglia	3.3	3.8	5.1	7.6	10.7	13.9	15.8	15.6	13.4	9.8	6.4	4.2	9.1
Monthly extremes:													Range
Valencia: max.	11.7	12.2	13.3	16.1	20.0	22.2	21.7	21.7	20.6	16.7	13.9	12.8	10.5
min.	-1.7	-1.1	-0.6	1.1	3.3	6.1	7.8	7.8	5.6	1.7	0.0	-1.1	9.5
Cambridge: max.	12.2	13.3	17.2	20.6	23.9	27.2	28.8	28.3	25.6	20.0	15.0	12.8	16.6
min.	-6.7	-6.1	-5.0	-3.3	-1.1	3.3	6.1	5.6	2.2	-1.7	-4.4	-6.1	12.8
Berlin: max.	8.1	9.6	15.8	21.0	29.0	31.1	31.6	29.7	26.3	19.8	12.2	8.9	23.5
min.	-11.9	-8.9	-5.9	-0.8	3.1	7.7	10.1	9.3	5.5	-0.1	-4.7	-8.7	22.0

<sup>1</sup> I am indebted to Dr F. Markgraf for the Berlin data. The British data are from the *Book of Normals*, Sections 2, 4, 5 and 6.

The approach to continentality at Cambridge is emphasised by the monthly extremes of normal maxima and minima (Table I and Fig. 3). The data for Cambridge are intermediate in some respects and extreme in others. The departure from oceanicity (Valencia) is shown by the greater annual range of the monthly extremes (Table I, last column), as also by the greater range of temperature in any month and by the greater differences between the summer maxima and between the winter minima. The values for the winter maxima and summer minima approximate. On the other hand, while Berlin shows a still greater annual range in the monthly extremes, Cambridge is peculiar in

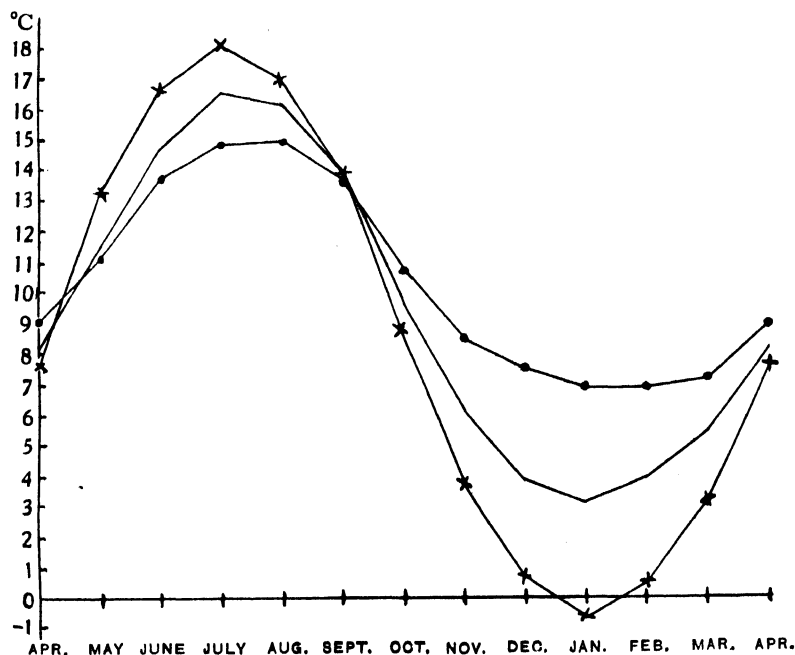


FIG. 2. Mean monthly temperatures at Berlin, Cambridge and Valencia. x — x — x Berlin, — Cambridge, • — • Valencia.

that it shows greater differences between the monthly maxima and minima in all months (except January and May) than Berlin. And Cambridge is further peculiar in having the highest winter maxima and the lowest summer minima of all three stations. An expression of this last feature is the extension of the period when frosts occur, for, while extreme minima below 0° C. are recorded for Valencia from December to March, for Berlin from October to April, for Cambridge they are recorded from October to May, and frosts lethal to young bracken fronds occur in Breckland as late as the first week in June. Frost is also a serious obstacle to the successful establishment of planted beech, larch and Douglas fir.

Another feature of significance may be mentioned here. A consequence of the oceanic impress on the climate of East Anglia is that there is no permanent

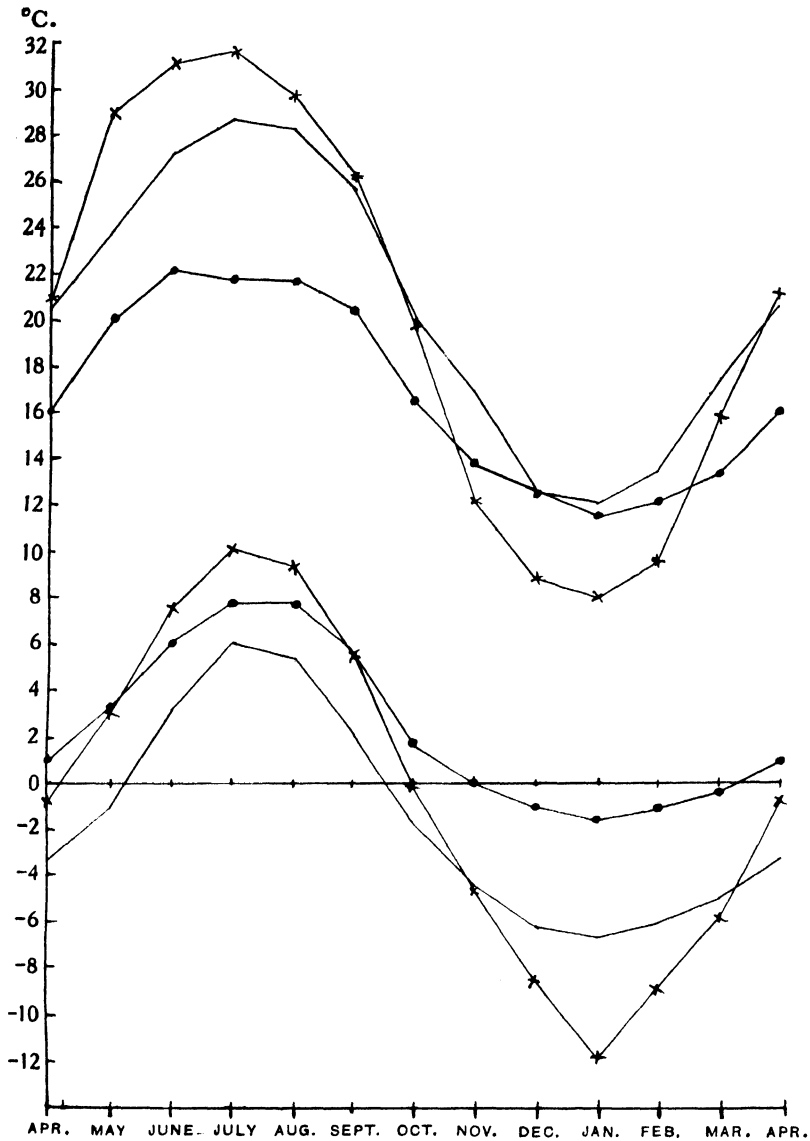


FIG. 3. Mean monthly extremes of temperature for Berlin, Cambridge and Valencia.  
 x — x — x Berlin, ——— Cambridge, ● — ● — ● Valencia.

snow cover during the winter months. Frosts may be severe, and hard bare frosts kill young bracken fronds and rhizome apices to a depth of at least 10 cm. from the soil surface. The phenomenon is not general because in most places protection is afforded by bracken or grass litter, or by a mat of lichen.

*Sunshine*

The summer flattening of the Valencia curve for extreme maxima (Fig. 3) is a reflection of the reduced number of hours of sunshine. The data (Table II) and curves (Fig. 4) for Valencia, Cambridge and Berlin show scarcely significant differences from October to April, but from May to September the differences are appreciable. Here again Cambridge falls between Valencia and Berlin—as it does for the daily average for the year—but shows significant differences from Valencia from June to September, whilst Berlin departs more widely from May to September, the September difference, however, being less for Berlin than for Cambridge.

Table II. *Mean daily number of hours of sunshine for Valencia, Cambridge, Berlin and East Anglia*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Valencia	1.55	2.45	3.97	5.33	6.55	6.27	5.13	5.00	4.43	3.26	2.17	1.32	3.96
Cambridge	1.71	2.66	3.90	5.53	6.52	6.70	6.52	6.06	5.03	3.35	2.07	1.29	4.29
Berlin	1.3	2.2	3.3	5.6	7.4	8.2	7.4	6.9	4.8	3.1	1.7	1.1	4.42
East Anglia	1.70	2.66	3.87	5.55	6.65	6.86	6.58	6.05	5.15	3.33	2.12	1.33	4.32

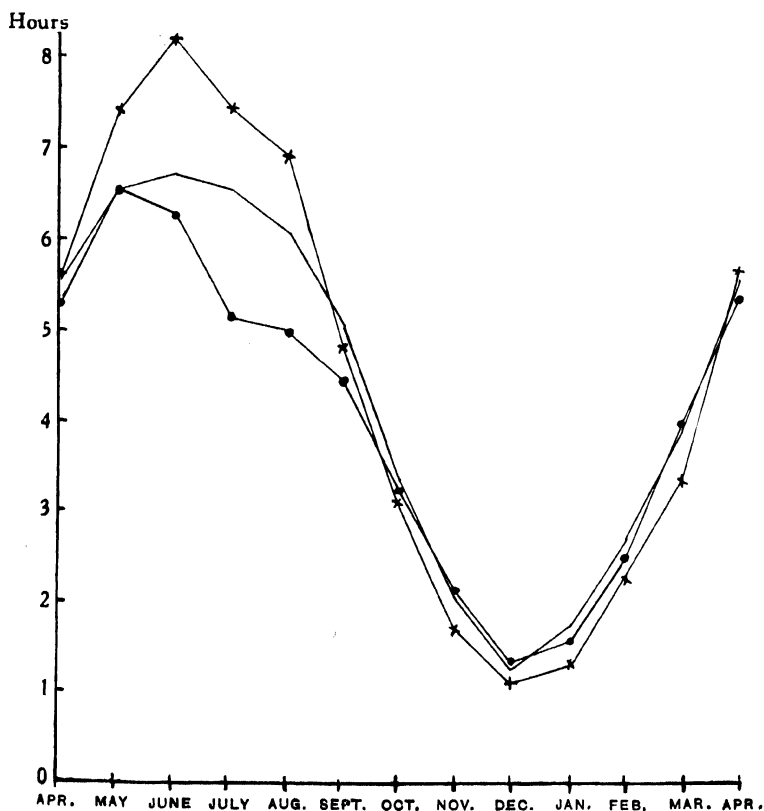


Fig. 4. Average daily number of hours of sunshine for Berlin, Cambridge and Valencia.  
 x—x—x Berlin, — Cambridge, ●—●—● Valencia.

*Rainfall*

Fig. 5 gives the curves for the monthly values of rainfall; the data are given in Table III.

Cambridge, like Berlin, has a low yearly total: Valencia has two and a half times as much, and its lowest monthly value is greater than the highest at Cambridge or Berlin.

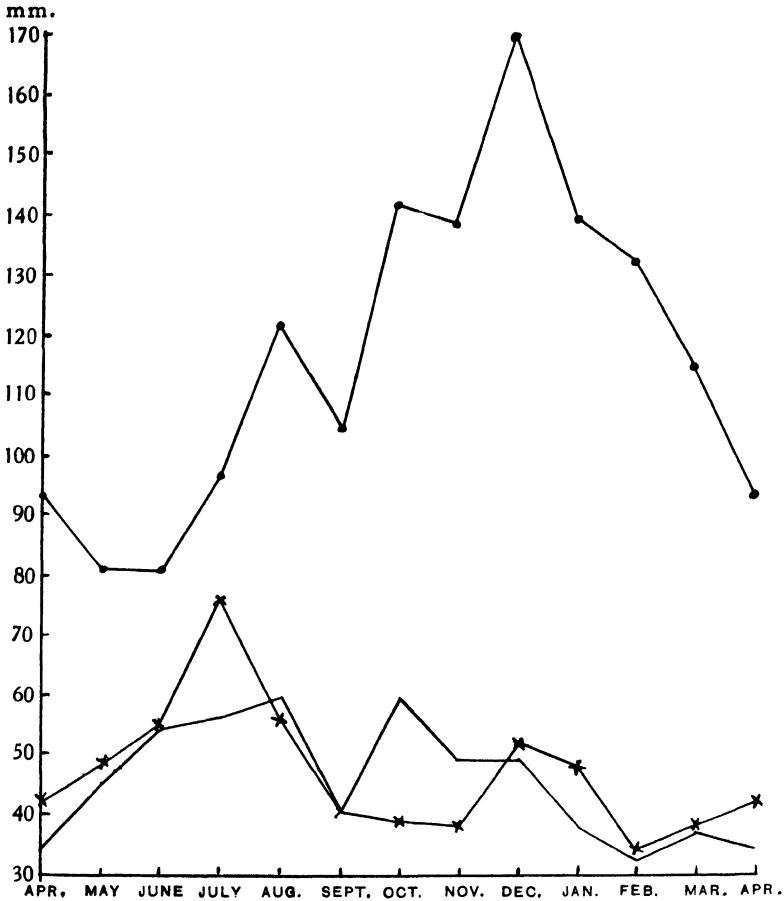


FIG. 5. Mean monthly rainfall for Berlin, Cambridge and Valencia. ×—×—× Berlin, — Cambridge, ●—●—● Valencia.

Table III. *Annual and monthly rainfall in mm. for Valencia, Cambridge, Berlin, Bury St Edmunds, Swaffham and East Anglia*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Valencia	139	132	115	93	81	81	96	122	105	142	139	169	1414
Cambridge	38	32	37	34	45	54	55	60	41	60	49	49	554
Berlin	48	34	38	42	49	55	76	56	51	39	38	52	578
Bury St Edmunds	46	38	48	39	46	53	64	66	51	69	58	61	639
Swaffham	47	40	45	38	44	54	65	66	54	73	62	61	649
East Anglia	46	39	43	38	46	51	59	56	48	67	59	58	610

The typical oceanic climate shows a summer minimum and a winter maximum, the typical continental climate the reverse. Cambridge falls between and alternately shows the continental and the oceanic influence in the ascendant. Even Valencia shows a slight continental influence in the steeper rise from the minimum in May and June to July and August, but returns to the typical oceanic curve in September with increasing amounts in the fall of the year to a December maximum, thereafter falling steadily to a minimum. Berlin shows a steep rise from April to a July maximum, followed by an equally steep fall to September, thereafter falling gently to November. Snow-fall presumably accounts for the higher values in December and January, after which there is a fall to the minimum for the year in February. From April to June Cambridge follows the Berlin curve fairly closely but fails because of oceanic influence to rise to the continental July maximum which is postponed till August; then the oceanic influence dominates in the low September and the high October value (a second maximum), but thereafter slowly yields in November and December to continental influence which dominates from February onwards to June. In Cambridge as in Berlin February is the driest month.

For Bury St Edmunds and Swaffham, just south and north respectively of Breckland, the annual rainfall is greater than at Cambridge, but its distribution throughout the year is much the same (Table III), the additional falls of 85 and 95 mm. being fairly evenly spread over the year except in the months of May and June, when the values are identical with those for Cambridge. Both places—at least the meteorological stations—are situated much higher: Bury at 226 ft. (68.9 m.), Swaffham at 250 ft. (76.2 m.), whilst Cambridge is at 41 ft. (12.5 m.).

For places within Breckland itself the following mean annual rainfalls are recorded:

Station	Height above O.D. in ft. (m.)	Mean annual rainfall in mm.
Mildenhall	50 (15.3)	562
Hengrave Hall	85 (25.9)	587
Santon Downham	32 (9.8)	617
Elveden	130 (39.6)	620
Thetford, Waterworks	170 (51.8)	605
Thetford, Ford St Gardens	44 (13.4)	594
Kilverstone Hall	70 (21.3)	551
Average		591

The average for these seven stations in Breckland is intermediate between the averages for Cambridge and for Bury and Swaffham, and there is no reason to suppose that the distribution of rainfall throughout the year is essentially different from that at these places just outside the area.

Thus Breckland falls between two stools. It is neither oceanic nor continental, and the combination of a high summer temperature with a rainfall which is low must be critical for many species unless there are compensating advantages. One of these is the relatively high humidity.

*Relative humidity*

The high values for Cambridge<sup>1</sup> (Table IV) are due to local conditions of topography and the high water table: those for Richmond (Surrey) are more likely to be a closer approximation to conditions in Breckland. Comparison shows that Valencia, Richmond and Berlin have much the same high values from October to January after which the curves (Fig. 6) diverge: the Valencia curve maintains a fairly level course, dropping only to the high minimum of 81 in May: the Berlin curve falls steeply during spring to a minimum of 65 in May and June, thereafter rising gently, whilst the Richmond values are more or less intermediate, the minimum of 72.9 occurring in June and July. It is possible that the relative humidity of the air over the dry soil of Breckland is even less than at Richmond, but no data are available to confirm this. The values may be critical for some species and may discriminate against the more exacting, whilst enabling the more tolerant of "Western European" species to survive (e.g. *Ulex europaeus*, *Genista anglica*).

Table IV. *Relative humidity at Valencia, Cambridge, Richmond and Berlin*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Valencia	86.3	85.5	83.7	82.0	81.0	81.5	83.7	84.6	84.3	84.3	86.0	87.2	84.2
Cambridge	90.6	89.2	84.7	82.1	78.2	77.7	78.3	79.8	83.6	87.4	90.0	91.4	84.4
Richmond	84.7	81.6	79.1	75.0	73.4	72.9	72.9	75.6	79.5	84.6	86.4	86.1	79.3
Berlin	86	83	78	69	65	65	68	70	75	82	85	87	76.1

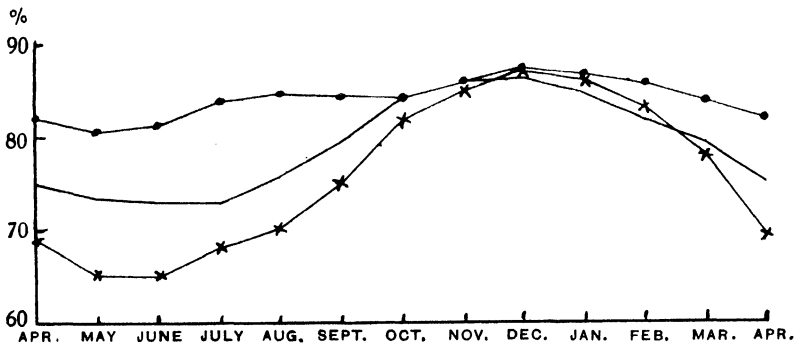


FIG. 6. Mean monthly relative humidity for Berlin, Richmond and Valencia.

× — × — × Berlin, — Richmond, ● — ● — Valencia.

*The N/S coefficient*

A general correlation exists between soil type and the N/S coefficient (Niederschlag/Sättigungsdefizit), that is, the ratio of the precipitation to the saturation deficit. The N/S coefficients for Valencia and Berlin are respectively 914 and 321. In the only reasonably detailed map (Fraser, 1933) for Great Britain showing the N/S distribution the 500 line appears to run through

<sup>1</sup> Average of the 11-year period 1924–34 worked out from data in the Monthly Weather Report of the Meteorological Office.



Breckland, but Dr Fraser informs me that the map is based on the averages of meteorological data for the 6-year period 1923–8, and for Cambridge this average figure is much higher than the 35-year average, due to the inclusion of the wet year 1924 with 728 mm. of rainfall. For the 10-year period 1924–33 the average annual temperature is the same as for the 35-year average (1881–1915), and the average rainfall only 6 mm. higher, so that the N/S quotient calculated on these data is likely to be nearer the general mean. This value is 409. For Richmond it is 322 (calculated from long period values), a figure which probably comes near the ratio for Breckland and is the same as the Berlin value.

In Tables I, II and III the mean monthly and annual temperatures, the mean daily number of hours of sunshine, and the annual and monthly rainfall for East Anglia (District No. 3 of the Weekly Weather Report) are given for comparison. These data are the averages of ten stations, of which seven may be described as coastal (with Norwich the most distant from the sea) and three only (Cambridge, Rothamsted and Tottenham) as inland. The values are therefore weighted by marine influence. Nevertheless they show the same general features as the data from Cambridge, Bury and Swaffham, and while Breckland, because of its light dry soil, may have a drier air and because of its low elevation a slightly lower rainfall than the neighbourhood to the north, east and south, yet the climate of the district is not peculiar to it but embraces a much wider area where other compensating advantages for plant growth, besides the assumed higher relative humidity and the slightly higher rainfall, are the high water table over much of the area and the water storage capacity of the soil. Where both are low, as in Breckland, the effects of the dry climate are accentuated, but the chief differentiating factor is the dry soil.

#### SOIL

##### *Geology*

In small patches the chalk appears on the surface, but practically the whole of Breckland is overlaid by glacial deposits. Until the whole area is worked over in detail in the light of recent views on the glacial epoch, the conclusions of Boswell (1931) for East Anglia may be applied. Of the four glaciations recognised by Boswell the second, represented by the Chalky-Jurassic Boulder Clay, appears to be widespread, covering the whole of Breckland: the third, represented by the Chalky Boulder Clay, appears to be much more localised. Between these two are found beds of sand, brick earth (loess) and gravel. The brick earth is local and much of it has been worked for brick-making: the gravel is also mainly local—and chiefly at higher elevations—but the extent of the interglacial sand is unknown.

As the boulder clays, gravels, loess and possibly interglacial sand outcrop the soils arising therefrom show considerable variation in chemical properties

but less so in physical. Much of the area is, however, overlaid by a blanket of wind-blown sand from a few centimetres to several metres in depth.

A general account only of the soils is given here: fuller details of the profiles will accompany the descriptions of the plant communities in later papers in this series.

*The origin of the sand and soil development*

Both Chalky Boulder Clays consist of chalk mixed with varying proportions of sand; the calcium carbonate content varies from about 40 to 65 per cent. By the leaching of the chalk the insoluble residue remains behind to form a sandy soil, since, except locally, the finer fractions, silt and clay, are negligible (approximately 1–3 per cent.). That this has happened and is happening now may be seen from the distribution of the calcium carbonate in three contrasted profiles (Table V, Nos. 1, 2 and 3, and Fig. 7, Curves 1, 2 and 3). These form a series of increasing soil depth. The underlying Chalky Boulder Clay contains from 40 to 50 per cent.  $\text{CaCO}_3$ , and each profile shows a gradually increasing percentage from the surface downwards. Further, the amount at the surface is smaller the greater the soil depth, so that the whole of curve 1 corresponds with progressively deeper levels in curves 2 and 3. The irregular distribution of flints in the profile is further evidence of the origin *in situ* of the soil. On the other hand, undisturbed blown sand overlying a soil whose  $\text{CaCO}_3$  distribution is similar to that shown in curve 1 shows an abrupt change at the plane of contact (No. 4 and curve 4). The blown sand is also free from flints.

Table V. *The profile distribution of  $\text{CaCO}_3$  in soils in situ and in drifted soils overlying Chalky Boulder Clay. The data are percentages of the soil fraction passing the 2 mm. sieve*

Soil depth in cm. ...	0–7·5	7·5–15	15–22·5	22·5–30	30–37·5	37·5–45	45–52·5
No. 1: in place	9·23	18·75	27·52	50·39	—	—	—
No. 2: in place	2·02	4·12	6·36	13·26	35·12	48·85	—
No. 3: in place	0·28	0·30	0·84	8·81	23·70	38·94	42·42
No. 4: blown sand (22·5 cm.) over chalky boulder clay	0·00	0·00	0·00	26·05	47·81	—	—
No. 5: "marled" blown sand (22·5 cm.) over chalky boulder clay	0·20	0·00	0·00	11·44	26·19	40·31	48·58

The puzzling occurrence in land which has never been cultivated of a layer of chalk stones sometimes on the surface of blown sand a few centimetres to 3 m. deep, sometimes in it, at 10–20 cm. or even greater depths, and sometimes on the surface of a truncated podsol, is explained by the use, in the past, of Chalky Boulder Clay on potentially mobile sand dunes to check further drifting. The chalk stones contained in the Chalky Boulder Clay behave like flints and may upon erosion of the sand below come to rest on the surface at any level in a soil profile (*vide* subsequent paragraphs). Curve 5, Fig. 7, shows the distribution of  $\text{CaCO}_3$  in a profile with scattered chalk stones in the surface few centimetres of a blown sand over Chalky Boulder Clay. An undisturbed

soil of this kind may, of course, have flints, introduced with the Chalky Boulder Clay, remaining behind after all the chalk stones have disappeared. Chalk was, of course, used in the past and still is to some extent in arable farming in Breckland: and chalk stones may be found in the surface soil long after the land has become derelict (e.g. part of Cavenham Heath).

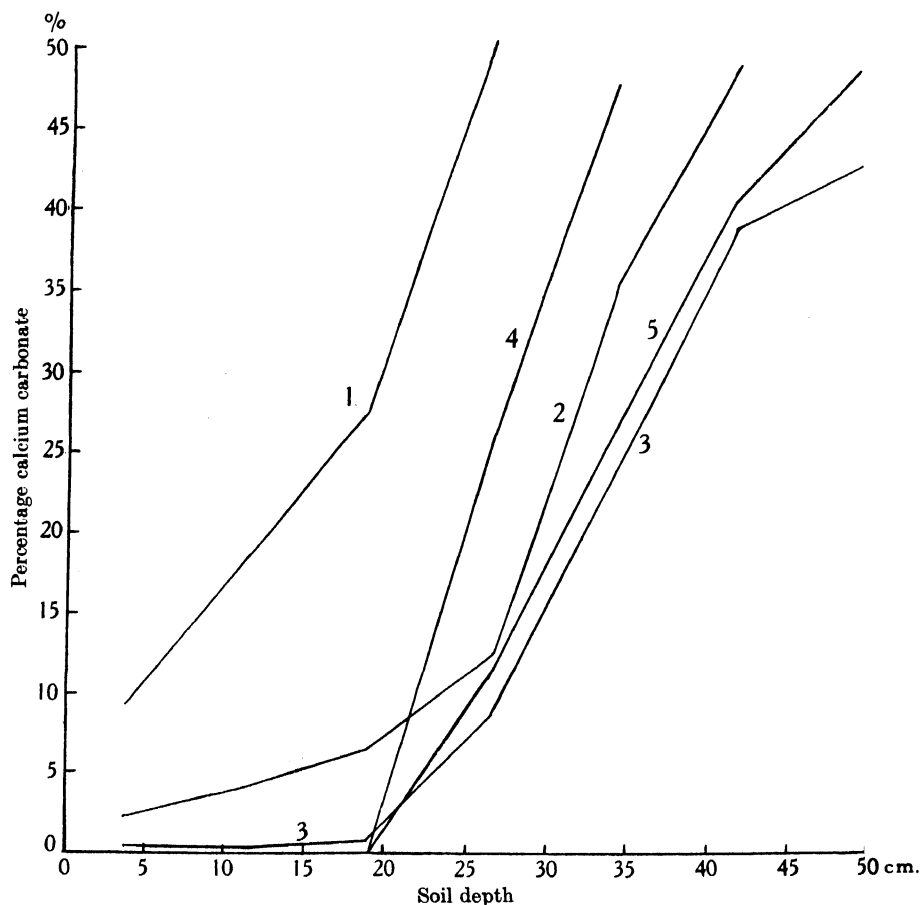


FIG. 7. Comparison between the distribution of  $\text{CaCO}_3$  in the profiles of soils *in situ* derived from the underlying Chalky Boulder Clay (curves 1, 2 and 3) and blown sand overlying the same Chalky Boulder Clay (curves 4 and 5). Note the gradual change in the one set, and the abrupt transition in the other. In example 5, the surface had at one time been "marled" to check blowing and a percentage of  $\text{CaCO}_3$  (too small to be shown on the scale adopted, *v. data*, p. 127) is found in the soil fraction passing the 2 mm. sieve.

In the leached soils the deficiency of  $\text{CaCO}_3$  in the surface soil and the change from an alkaline to an acid reaction initiate the mobility of the sesquioxides of iron and aluminium and render possible their transference to lower layers. In the field the profile corresponding to curve 3 shows a distinct, reddish, B horizon. The laboratory data confirm the beginnings of sesquioxide

accumulation; the percentage values for successive samples at intervals of 7.5 cm. from the top downwards are 1.10, 1.12, 1.41, 1.74, 2.05, 2.02, 1.38. Depletion of  $\text{CaCO}_3$  and hence of substances buffered against acid will be followed by an acceleration of the podsolising process, and weakly podsolised soils will rapidly change to profiles with well-marked A and B horizons.

Podsols in all stages of development do, in fact, occur, and well-developed examples are found at low levels as well as high (over 150 ft. (46 m.)). The most heavily podsolised soils appear, however, to be confined to the low ground (under 50 ft. (c. 15 m.)), and excellent examples occur in the valleys of the Lark and the Little Ouse and the low ground fronting the Fen: they are also found under it along its eastern margin. An extreme example in the valley of the Little Ouse shows a B horizon 76 cm. thick immediately overlying Chalky Boulder Clay; another in the same valley a B horizon of about 50 cm. and a reticulum of "B" lines in C down to a depth of at least 3 m. from the surface of the existing B. The existence and nature of this heavily podsolised soil raise several problems. How old is it, under what conditions was it formed,<sup>1</sup> what relation does it bear to the water table and are the well-developed podsols at high and low levels of the same age and nature? As to its age, the only fairly certain information is that it existed before the formation of the Black Ditches on Cavenham Heath. If this earthwork is part of the same system as Fleam Dyke and Devil's Dyke it dates from the period A.D. 400–700, but Mr Lethbridge informs me that there is no internal evidence to prove this. The podsol, however, is probably much older. Further observation is needed to answer this and other questions.

In many profiles the A horizon is not deep enough nor bleached enough to account for the great development of the B. There is, in fact, in most a sharp line of demarcation between the B horizon and the existing A: they are often separated by a layer of flints. And this flint layer is also found in weakly podsolised soil as well as on the surface of podsolised and unpodsolised soils alike. The discontinuity arises from erosion following loss of coherence due to the removal first of calcium carbonate and later of iron. The sand particles thus freed are dried and blown away. The phenomenon may be seen on highly calcareous soils where the plant cover is discontinuous and the soil is maintained in a young state by surface erosion with the consequent accumulation at the surface of flints too heavy to be blown or washed away. But it is more obvious in old podsolised soils where the degeneration of the plant cover over large or small areas exposes the soil to erosion by wind and heavy rain, especially after a dry spell. Stones too heavy to be moved, accumulate at each new surface until the cessation of erosive action for a period long enough to allow a plant cover to become established checks a continuation of the process,

<sup>1</sup> In Holland a similar podsol is found. **Beijerinck** (1934) considers the *Humusortstein* to have been formed under arctic conditions in immediately post-Glacial times. I am indebted to Dr E. M. Crowther for the reference.

or until the stones form a protective layer—a desert pavement—preventing further erosion. In this way the profile is truncated and capped by a layer of flints, the level at which it occurs varying with the number of flints, the resistance offered by the soil itself to further erosion and the intensity of the erosive forces. In many places it appears near the upper limit of the B horizon: in some lower down, bringing the base of inverted “cones” formed by the truncated finger-like downward extensions of the B<sub>2</sub> horizon near to the surface; and in others in the C horizon, with B lines in C as evidence of a pre-existing B.

The sand removed by erosion is deposited elsewhere, covering uneroded soils and soils truncated by previous erosion, the layer of gravel marking the plane of contact between drifted soil and soil *in situ*. This drifted sand varies in depth from a few centimetres to several metres, and it in turn is subjected to the podsolising process. Where it is relatively thin, overlying a soil eroded down to the B horizon, it forms a new A horizon, whose humus and sesquioxides add to the existing B. Thus the marked B horizon found in Breckland may in part at least be due to a succession of A horizons, whose cycle of change may be summarised as drifted sand, a period of stability and leaching following plant colonisation, soil exposure and erosion following the disruption of the vegetation cover. In places the blown sand is deeper and may show one or more incipient podsols one on top of the other in a succession of drifts.

Thus the sand which forms the present surface may be derived in part directly from the Chalky Boulder Clay, in part directly from the Chalky-Jurassic Boulder Clay, and in part from the interglacial sand, itself derived by decalcification of the Chalky-Jurassic Boulder Clay during the subsequent interglacial period. There is no need to postulate an external origin in the sandy shores of an ancient Fenland sea: in fact, the distribution of flints in the profile excludes this origin for most of the sand. For the drifted sand without flints the internal origin suggested adequately explains its presence.

Physically the soils of Breckland, apart from those where the water table is near the surface, are, with few exceptions, coarse textured, dry and permeable. Chemically they range from highly alkaline young soils with much CaCO<sub>3</sub> to extremely acid old soils with none. And not only are these soils in different stages of development but the drifted sand shows chemical variation according to its age and its origin in a young soil or in the A, B or C horizons of an old one. The flora and vegetation show corresponding differences.

The geological evidence makes it highly probable that there was similar soil variation in the interglacial periods following the Chalky-Jurassic Boulder Clay. Thus if, as Wilmott contends, much of our British flora survived the last onset of the ice, calcicoles as well as psammophiles had the soils they preferred during the last interglacial in Breckland (cf. Salisbury, 1931). It is also likely that leaching of the soils since the Glacial Period has changed the relative proportions of calcareous to non-calcareous soil, although erosion

maintains to this day many hundreds of acres of calcareous soils. Any speculations about the past flora and vegetation of Breckland must take this into account.

#### VEGETATION

In phyto-geographical studies different authors have dealt with the parts played by climate, soil and plant competition: the last two are often neglected or passed over with a bare mention. In his analysis of the flora of East Anglia, including Breckland, and in his assessment of the contributions made to it by species whose "Massenzentra" lie in different parts of Europe, Salisbury (1931) gives soil and plant competition due notice along with climate. For a proper understanding of the flora of Breckland, or, for that matter, of any region, all three must be taken into account, emphasis being placed now on one, now on another, as the local conditions of microclimate, soil and plant competition dictate.

The flora of Breckland is essentially drought resistant or drought escaping (e.g. the early flowering annuals). But the continentality is not so marked as to exclude the more tolerant oceanic species, *Carex arenaria*, *Erica tetralix* (wet places), *Genista anglica*, *Tillaea muscosa*, *Ulex europaeus*—all xeromorphs—are found in Breckland. The soil conditions undoubtedly exclude many species which could tolerate the climate, but the way the climate differentiates between species may be illustrated by reference to *Erica cinerea* and *Calluna vulgaris*, both species tolerant of infertile soils. From Breckland, the West European *Erica* is absent, the more tolerant *Calluna* with its greater range eastwards in Europe, is present in abundance. But its reduced vigour, poor flowering, and its inability in some places at least to maintain itself indefinitely (quite apart from rabbit grazing) contrast strongly with its luxuriance in the damper climate of the west and north. Its behaviour is in fact comparable with that in Jutland and the north-west German plain.

There can be little doubt that the larger numbers of hours of sunshine (and perhaps the quality of the light) condition the presence of the "steppe" species, as Salisbury has deduced from a comparison of the production of fertile seeds in *Silene conica* and the meteorological factors during the period of his observations. But within the area rendered possible to them by climate, their distribution is far from general, and there is evidence to show that some, at least, of these "steppe" species are confined to young soils—as in fact many of our rarer species are, e.g. some "arctic-alpines" and Mediterranean species.

It is also true that many of these rarer species are in this country restricted to open plant communities. In Breckland many of the communities, on calcareous and non-calcareous soils alike, are open, and it is in these that the annuals (proper to the soil type) are found in greatest profusion. Overgrazing of closed communities likewise produces and maintains the opportunity for their establishment and persistence. Abandoned, as well as cultivated, arable land offers a similar opportunity.

In adjoining areas with similar climate, but with damper soil and greater competition from plants more at home in the area, they are absent: but wherever the soil conditions of Breckland are reproduced, e.g. on gravels near Cambridge, the assemblage of plants is similar and includes some of the rarer "continentals". It is possible that keen competition in closed communities excludes them from some habitats otherwise suitable. Experiment alone can decide.

Apart from the plant communities influenced by a high water table, e.g. the transitional "Fen-Breck" vegetation, the vegetation of Breckland is a patchwork of—mainly—four major plant communities dominated respectively by *Festuca ovina* and *Agrostis tenuis* (*vulgaris*) and *palustris* (*alba*), *Carex arenaria*, *Calluna vulgaris* and *Pteridium aquilinum*. These communities are not uniform among themselves and the Festuco-Agrostideta on calcareous soils and on very acid drifted sands overlying a truncated podsol are as far apart in floristic composition as the grassland on the chalk of the South Downs and on the neighbouring Lower Greensand, to each of which the Breck communities respectively do in fact bear a close relationship. The communities on calcareous soils contain about ninety species of higher plants, including many calcicoles, while those at the other extreme comprise about a dozen species, all common plants of acid soils. There is in fact a large number of fescue-bent communities, differing from each other in floristic composition, physiognomy and ecological structure, forming a series in the edaphic succession from soils with much  $\text{CaCO}_3$ , through soils in which it is deficient, to soils from which it is absent.

#### *Successional relationships*

Whilst some kind of Festuco-Agrostidetum is found in any soil type and in any locality in Breckland, the same cannot be said of the *Carex*, *Calluna* and *Pteridium* communities. The range of these species is less and their dominance is still more restricted. *Carex arenaria* is found over a wide range of soils, acid and alkaline alike, but it is less widespread than the other two and it shows a high degree of association with relatively recently drifted sand, on which alone it is really dominant: *Calluna* covers considerable areas, is widespread, and its presence in a Festuco-Agrostidetum probably means potential dominance, but it is absent from highly calcareous soils; whilst *Pteridium* alone shows a range of soil tolerance almost equal to that of *Festuca ovina* and *Agrostis palustris*, but it is excluded from "frost holes" and its presence in a Festuco-Agrostidetum in other areas cannot be assumed to imply ultimate dominance. From soil type to soil type their frequency varies with their vigour: in height *Carex* varies from 8 to over 30 cm., *Calluna* from 15 to 91 cm., and *Pteridium* from 30 to 150 cm.

*Carex*, *Calluna* and *Pteridium* are highly social and aggressive species; *Pteridium* particularly so. All three reproduce vegetatively and by seed or

spore, but in sedge and bracken vegetative reproduction is more important and in heather reproduction by seed. The dispersal of bracken is restricted by the rare reproduction from spores, but dispersal by seed gives sedge and heather an opportunity of colonising ground previously without them. Now each of the different kinds of Festuco-Agrostideta may be regarded as the starting point of a sere with *Carex*, *Calluna* and *Pteridium* as potential invaders and possible dominants replacing the Festuco-Agrostidetum. But from what has been said it is clear that what happens will depend on the local conditions of soil and microclimate. For example, the limitations imposed by the most highly calcareous soil will exclude *Calluna* but not *Carex* and *Pteridium*. These, however, never become dominant, so that as long as the soil remains as it is the Festuco-Agrostidetum is the ultimate stage. In frost holes bracken is excluded and the Festuco-Agrostidetum proper to the soil may be replaced by *Carex* or by *Calluna*: but again the soil differentiates, for on a recently drifted unleached sand *Carex* succeeds and becomes dominant and on the B horizon of a truncated podsol, *Calluna*. In other areas the fescue-bent community may give way to bracken. Moreover, as the relationship between the Festuco-Agrostideta on the one hand, and *Carex*, *Calluna* and *Pteridium* on the other varies, so, from soil type to soil type, the relation between *Carex/Calluna*, *Carex/Pteridium* and *Calluna/Pteridium* also varies. Aggressive as bracken is, it must not be supposed that where sand-sedge and bracken are found together, bracken will as a matter of course ultimately dominate. In fact, areas of *Carex* occur from which the *Pteridium* has been ousted, as the rhizome remains in the soil testify. Thus there is no simple dynamic relationship between the aggregate Festuco-Agrostidetum and its possible successors.

Many of the phenomena of succession deduced from the observed relationships between the Festuco-Agrostideta and *Carex*, *Calluna* and *Pteridium* are really cyclic. Even in some kinds of fescue-bent communities patches of the vegetation show a cycle of change, progression, dominance, retrogression. And the same phenomena are demonstrated by *Carex*, *Calluna* and *Pteridium*. Cyclic change in *Carex* is the least well attested, but certainly with age and the accumulation of humus *Carex* vegetates and flowers less profusely—similar behaviour is well known on coastal dunes—and areas exist where it has died out, and where overgrazing can scarcely be held responsible. The rise to dominance of *Calluna*, followed by death and disruption of the community is a striking phenomenon on Tuddenham Heath; and rabbits have not caused the death of the heather. By the wholesale annihilation of the heather large areas will in time be laid bare and exposed to erosion, as smaller areas are now. On soils thus exposed a new Festuco-Agrostidetum is built up. *Pteridium* shows a similar phenomenon in the wave-like advance on a fescue-bent community. The crest of the wave coincides with bracken dominance and the local extinction of the grass communities. A short distance beyond the crest, grassland reasserts its dominance, though bracken, reduced in size and number, remains



a constituent. Thus there are good reasons for regarding the aggregate *Festuco-Agrostidetum* as the fundamental, relatively permanent, community in Breckland, the others enjoying a temporary dominance. But it remains to be seen whether this is true under all conditions as it is certainly true under some.

It is believed that the cyclic phenomena just described in barest outline are the result of the plants' reaction to the dry conditions of summer. But their temporary occupation of the ground may leave a transient or permanent impress on the soil, depending on the soil itself, the species, the kind of humus it forms and its arrest, retardation or acceleration of the process of podsolisation. The case of *Calluna* seems clear: a succession of cycles including *Calluneta*, leads to the acceleration of podsolisation and of the edaphic succession. The case of *Pteridium* is not so simple. There is no evidence that bracken itself brings about soil degeneration, for its humus contains much potassium, but its presence in a grassland not only discourages rabbit grazing but probably promotes the growth of the grasses themselves. Thereby more humus is added to the soil and in this and probably in other ways soil leaching is promoted. How far the process of podsolisation would proceed under the fescue-bent communities alone is not known: probably the later stages of podsolisation are mainly the work of heather communities.

The unravelling of the tangled skein of plant communities and the interpretation of their successional relationships are rendered more difficult by the varying intensity of rabbit grazing. But the simple explanation offered by Farrow (1915) that the distribution of fescue-bent, sand-sedge, heather and bracken communities is determined by the intensity of rabbit grazing, soil playing no part, is true only up to a point, for it obscures the primary differences determined by soil. Valuable as was the advance made by Farrow in establishing and stressing the importance of the biotic factor, the facts already given are sufficient refutation of his sweeping generalisation. Fuller details will be added in further studies. Meantime, it may be observed that no amount of rabbit grazing will reduce to a common level the fescue-bent on highly calcareous soils and on heavily podsolised sands, nor does Farrow's explanation account for the varying behaviour of bracken, which is unpalatable to rabbits, nor, for that matter, of sand-sedge and heather where grazing is negligible. The intensity of rabbit grazing is important, however, in determining the limits of the sedge, heather and grass communities where these occur *on the same soil type*, i.e. in the same sere. But the soils of Breckland are not uniform, not even on Cavenham Heath.

The use of the term *destructive* as applied to rabbit activity is open to serious objection, for it is ambiguous. Activities which are destructive by bringing about the replacement of a later stage of the succession by an earlier may equally well be described as *maintaining* or even *constructive* from the point of view of soil fertility. The point of view therefore must be defined, and since vegetational and soil development proceed ultimately in the direction of an

impoverished flora and a podsolised soil, rabbit activity may be described in relation to that process as retrogressive, maintaining or accelerating. Thus rabbit grazing of the fescue-bent community on the most highly calcareous soil is maintaining, for the open community is kept young by erosion because it is kept open, and the removal of leaves and shoots prevents the accumulation of humus and the acceleration of leaching. Again, heavy grazing of a *Callunetum* causes retrogression of the vegetation to an earlier stage in the sere and may also lead to retrogression of the soil by the disruption and removal of the acid humus of the soil horizon  $A_0$ . Yet again, soil retrogression follows the throwing of unleached soil to the surface and communities thereon represent an earlier stage in the edaphic succession than on the same soil left intact. There is no evidence so far available to show that rabbit activity accelerates soil and vegetational development.

Besides the four major communities there are the earlier stages in the succession on recently eroded and drifted soils. Mosses and lichens play an important part and within the general succession cyclic phenomena are again exhibited. But eventually the succession leads to a *Festuco-Agrostidetum*, or if *Carex* is in the neighbourhood to one with much *Carex* or with *Carex* dominant (on blown sand). If the horizon B is exposed at the surface *Calluna* is found instead of *Carex*.

### *Human influence*

The influence of the past lives in the present and no account of the vegetation would be complete even in an introductory outline without some reference to the reaction of the vegetation to past climates and human activity. The absence of a fossil record makes deductions about the past flora and vegetation highly speculative, but the study of the peat which overlies a podsol in the transitional "Fen-Breck" vegetation may be expected to provide a clue to the period before which podsol formation took place. The discovery of human artefacts, useful in dating a geological deposit, has however to be interpreted with caution in assigning an age to a podsol, for podsolisation may take place after the artefacts arrive at the place of discovery.

In the fluctuations of climate in post-Glacial times the higher rainfall of the Atlantic period would remove one of the chief restrictions to plant growth and permit a wider range of representation of plant forms on the soils then available, and it is possible that trees grew naturally on the Breck. But from what is known about the type of country inhabited by Neolithic man it is unlikely that there was anything like dense forest. The discovery in Grimes Graves of charcoal of oak, beech, pine (Reid, 1914), alder, hazel, whitebeam and yew<sup>1</sup> cannot legitimately be used to support the assumption of the existence of forest. Even the floristic value of the discovery is diluted, for it merely

<sup>1</sup> From charcoal supplied by Mr A. L. Armstrong. I am indebted to Mr F. Jane for the identification of whitebeam and yew.

proves that early man had access to these trees and they may quite well have been obtained in adjoining wooded areas, e.g. "Fenland" or neighbouring stream banks. At the same time if we assume (and I think the assumption is justified) that soils similar to those of to-day existed in (say) Atlantic times, I see no reason for supposing that the Breck was treeless because trees couldn't grow there. Birch, pine, oak, beech, all regenerate in Breckland to-day and they may equally well have done so in the past. But it is likely that if forest existed it was of a kind which Neolithic man could easily handle. Furthermore, the soil studies suggest that a much higher proportion of the area was at one time occupied by shallow calcareous soils, unfit to bear forest but to which grassland is proper.

The relatively large population of Breckland right down to and including Anglo-Saxon times and the necessity for throwing up defensive earthworks (Fleam Dyke, Devil's Dyke) across the narrow grassland gateway from the south-west, point to an absence of natural forest barriers and places of retreat. But the first written record is contained in the Little Domesday. From the information contained therein Darby (1934) has constructed a map showing the distribution of woodland in East Anglia in 1066—the woodlands being assessed in terms of pannage for so many swine, the numbers 80 and 500 being chosen as index figures to show "moderate and large amounts of wood respectively". In this map Breckland shows no woodland except at the localities mentioned below, and these are "80 pig" woods. Fuller details for Norfolk are given by Beevor (1925) in a map showing the distribution of wood for 100 pigs in 1086. The places in or near Breckland are Hockwold-cum-Wilton, bordering on the Fen, and Hockham, Ashill, and Carbrooke at Breckland's north-eastern limits. The only place *in* Breckland is Langford, which is also shown as carrying some wood in Faden's map of 1790, a date before planting became usual. Langford, however, lies on the Wissey and the woodland may have been of the valley fen type. Beevor also makes the interesting computation that one to two acres of wood supplied pannage for one pig, so that Langford wood must have been something like 100–200 acres in extent. At the date of the compilation of Domesday Breckland was therefore essentially woodless, and so it appears to have remained until widespread arable cultivation following enclosure led, early last century, to the formation of belts of woodland of conifers and broad-leaved trees, and hedges of pine and spruce to check the blowing of the sand from the tilled fields.

The former export of barley, wheat and raw wool from East Anglia to the Low Countries, themselves in close trade connection "with the Hanseatic organisation of the Baltic and the Venetian organisation of Mediterranean and Eastern trade", bears witness to the agricultural importance of the area, in which Breckland, "long famous as a sheep district", had its share (Roxby, 1928). The intercourse was facilitated by the navigation by barges of the Little Ouse and the Lark as far as Thetford and Bury respectively, and this fact

ought to be kept in mind when the migration and distribution of species are under consideration.

At the present day sheep grazing and arable cultivation are much restricted. According to Clarke (1925), land under cultivation in the 13th, 14th and 15th centuries now bears "heath". The same authority considers that most of Breckland was at some time or other cultivated; and there are indications from other sources that some areas at least which now bear natural vegetation were once under the plough. The abandonment of arable cultivation may have been due to purely economic causes or to soil impoverishment or to both combined. The supplanting of earlier methods of land fertilisation, marling and "natural" manuring, by the use of artificial manures on soils deficient in water and lacking in the absorbing complexes, clay and humus, is not conducive to the production of good crops. Ploughing of calcareous soil breaks the leaching gradient but it also promotes disintegration of the chalk and its more rapid disappearance from the upper layers. Impoverishment must then be rapid unless fertility is maintained by marling and the introduction of humus to hold the artificial fertilisers.

Be that as it may, much land has gone out of cultivation and has been acquired by the Forestry Commission (approximately 40,000 acres in 1934). The birth of a dense forest, mainly of *Pinus silvestris* and *Pinus nigra* var. *calabrica* (Corsican Pine) in an area for long unforested marks the biggest change in Breckland's vegetational history. The growth of the forest, the play of the varying complex of microclimatic, soil and biological factors upon it, the repercussions of the forest on these and on the fauna and flora—the elimination of some species, the introduction of others and the readjustments among the survivors—these, as well as the intimate study of the forest itself, including problems connected with its establishment, maintenance and rejuvenation, present an unrivalled opportunity for the study of a forest in the making. Nor is this all. The coming of the forest will alter the economic life of the area and calls for creative skill in adjusting and harmonising existing interests with those of the newcomer. The materials are ripe for record in a modern Domesday, invaluable to all interested in land utilisation.

The work to which this is an introduction cannot be carried out without free access to all parts of Breckland. It is a pleasure to acknowledge my indebtedness to the proprietors who have willingly granted me permission to traverse their land, and in particular to H.M. Forestry Commission, the Duke of Grafton, Lord Iveagh, Lord Fisher, General Home, L. D. Wigan, Esq., and Brig.-Gen. Lotbinière. To Lord Iveagh's agent, Mr Dow, I am indebted for much assistance.

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## REFERENCES

- Beevor, Sir Hugh.** "Norfolk woodlands from the evidence of contemporary chronicles." *Quart. J. For.* **19**, 1925.
- Beijerinck, W.** "Humusortstein und Bleichsand als Bildungen entgegengesetzter Klimate." *Proc. Kon. Akad. Wet. Amst.* **37**, 1934.
- Boswell, P. G. H.** "The stratigraphy of the glacial deposits of East Anglia in relation to early man." *Proc. Geol. Ass., Lond.*, **42**, 1931.
- Clarke, W. G.** *In Breckland Wilds*, London, 1925.
- Darby, H. C.** "Domesday woodland in East Anglia." *Antiquity*, **8**, 1934.
- Farrow, E. P.** "On the ecology of the vegetation of Breckland." *This JOURN.* **3**, 1915.
- Fraser, G. K.** "Studies of Scottish moorlands in relation to tree growth." *Bull. For. Comm.*, Lond., No. 15, 1933.
- Harmer, F. W.** "The Pleistocene Period in the eastern counties of England." In *Geology in the Field*, ed. by H. W. Monckton and R. S. Herries, 1910.
- Reid, C.** In *Prehistoric Society of East Anglia*, 1914.
- Roxby, P. M.** "East Anglia." In *Great Britain, Essays in Regional Geography*, ed. by A. G. Ogilvie, 1928.
- Salisbury, E. J.** "The East Anglian flora." *Trans. Norfolk and Norw. Nat. Soc.* **13**, 1931-2.

# THE BRYOPHYTES AND LICHENS OF BRITISH WOODS. PART I. BEECHWOODS

By W. WATSON

## INTRODUCTION

ONE of the first attempts to show that bryophytes were important constituents in an ecological survey was "The bryophytes of the woodlands of Somerset" (Watson, 1909). Since that was written much work has been done on the bryophytes of woods, and many ecological articles on woods have given lists of the bryophytes while a few have mentioned the lichens as well. Most of the work has been of rather haphazard character, because the ecologist has often had a hazy or incomplete knowledge of bryophytic field work and has merely collected samples of what appeared to be the most prominent bryophytes and lichens in the area studied and sent them to experts for determination. This collecting has also usually been done at the same time as the phanerogamic flora was examined, whereas it is much wiser to examine the phanerogamic and bryophytic floras at different times. From long experience I have found that bryophytic work is done more quickly and accurately when the larger phanerogamic plants are ignored and the eye and mind are habituated to deal with the smaller plants only. Then again the dependence on an expert may give an erroneous impression of the frequency of a plant. It is quite easy for a collector to send a specimen of a relatively rare plant under the impression that it forms a conspicuous portion of the mossy carpet. In some cases the bryophytes have been determined by the collector. On the whole this method has worked much better, except for a few cases of wrong determination. As an example the following may be mentioned. *Polytrichum commune* is often given for dryish places in woods, but the species found is almost certainly *P. formosum* since *P. commune* is usually found in very wet places and is rarely a woodland plant. Richards (1928) gives *P. commune* as occurring on a path side in a Middlesex wood, but his remarks show that he considered the circumstance was exceptional and abnormal. Other instances will be noted when dealing with the various kinds of woods. In some cases mosses of the woodland border have been included in the actual flora of the wood, and occasionally a rare bryophyte of the district has been included though it is not a usual woodland plant. On the whole the lists are fairly accurate but usually incomplete.

The "Woodlands of Somerset" (1909) gave a list of the main bryophytes found in three different types of wood: oak, oak-hazel, and ash. The lists for the oakwoods are characteristic of the *Quercus sessiliflora* woods of Somerset, whilst those for the oak-hazel woods are characteristic of the pedunculate oakwoods in which hazel (and sometimes ash) is frequently present. The article was written in order to show that the three chief kinds of woods in Somerset had a differentiated bryophytic flora as well as a differentiated

phanerogamic flora. Since it was written much work has been done in other parts of the British Isles, and in this article the more recent work has been incorporated and correlated with the earlier. Some reference was made in the Somerset paper (1909) to oakwoods in which pines were present and to beechwoods. As the reference to the latter was very brief they will be dealt with first and further details for other types of woods will be given in Part II.

#### BEECHWOODS

Characteristic examples of beechwoods do not occur in Somerset, and the brief reference to them in the earlier paper is of little value except in regard to the paucity of bryophytes. *Fissidens taxifolius*, *F. bryoides*, *Mnium undulatum*, *Brachythecium rutabulum*, *Eurhynchium praelongum*, *Hypnum cupressiforme*, and *Frullania dilatata* were given as present. In the beechwoods of other parts of England the same species are present when the soil is basic or neutral. In some beechwoods on acid soil the species of *Fissidens* are rare or absent.

The beechwoods of the Chalk proper (i.e. on the shallow soils of the Chalk escarpments and valley sides) and of the Chalk Plateaux of Hampshire were investigated by Adamson (1921) and those of the Chalk Plateaux of the South Downs by Watt (1924, 1925). As the beechwoods of the Chalk proper are on basic, those of the Plateau on more or less neutral, and those of the Eocene basin on acidic soils, they ought to be taken in the natural sequence indicated, but for several reasons, chiefly related to my personal and detailed investigation, those of the Plateaux will be considered first. Those on the Goodwood estate were described and some preliminary work on bryophytes given by Watt, who, later on, kindly conducted me over the woods and pointed out the chief features mentioned in his papers.

#### *Beechwoods of the Chalk Plateaux*

The succession is briefly summarised as follows: Grassland → Scrub → Associates → Ash-oak associates → Beech associates → Beech consociation, which is the climax forest type. The soil is more or less neutral, or slightly acid, and seldom shows much free calcium carbonate. The woody plants of the scrub consist chiefly of hawthorn, blackthorn, dogwood, white beam, ash, oak and gorse, with ling and heather sometimes becoming frequent. The woody plants of the ash-oak associates are mostly ash and oak, but sometimes beech, or yew become abundant. The Beech associates has the beech as the dominant tree, but oak and ash are present and sometimes abundant. The beech consociation is relatively a pure beechwood containing at least 90 per cent. of beech. Three successional series or seres, each on a different depth of soil, were distinguished by Watt. Sere 1 has the greatest depth of soil, sere 2 an intermediate depth, whilst sere 3 has a shallow layer of loamy soil, often less than 6 in. deep, over the chalk. In the beechwoods themselves there is not any, or very little, ground flora at first, then *Oxalis* appears and finally *Rubus*. These three stages

in the history of the beechwood are therefore distinguished as (a) bare stage, (b) *Oxalis* stage, (c) *Rubus* stage. In a beechwood belonging to sere 2 the bare stage probably lasts about 75 years: during the next 25 years the wood is in the *Oxalis* stage, and after about 100 years *Rubus* (often *R. vestitus* or *R. rudis* though other *Rubi* occur) begins to be conspicuous in the undergrowth. Since Watt showed that the phanerogamic constituents of these seres and stages vary, attempts were made to differentiate them by their bryophytes and lichens, but with indifferent success. The differences of depths of soil in the seres do not affect these plants directly, but some indirect effects, due to the possibility of a greater water reserve or of greater leaching in the deeper soil, were expected. The growth of *Oxalis* or *Rubus* as the wood gets older may be expected to eliminate some of the constituents of the moss stratum, but on the other hand the better fixation of the ground may provide the bryophytes with better opportunities of establishing themselves. The leaching may be sufficient to allow species which usually occur on non-calcareous soil to grow, and there is evidence for this, especially on banks by the sides of the "rides" or on the margins of the woods, though indifferent or calcicolous plants are intermixed.

In the beech consociation (sere 3) the following bryophytes occurred on the ground with *Digitalis* in the neighbourhood of planted pines:

<i>Brachythecium purum</i>	f.	<i>Mnium hornum</i>	f.*
<i>B. rutabulum</i>	o.	<i>M. rostratum</i>	f.
<i>Eurhynchium abbreviatum</i>	o.	<i>M. undulatum</i>	f.
<i>E. praelongum</i>	f.	<i>Plagiothecium denticulatum</i>	f.
<i>Lophocolea cuspidata</i>	f.	<i>Polytrichum formosum</i>	f.

\* In larger patches than usual.

On the ground in the coppice the following plants were growing together:

<i>Agrostis tenuis</i>		<i>Lonicera periclymenum</i>	
<i>Digitalis purpurea</i>		<i>Luzula forsteri</i>	
<i>Euphorbia amygdaloides</i>		<i>Pteris aquilina</i>	
<i>Fragaria vesca</i>		<i>Rubus argenteus</i> <sup>1</sup>	
<i>Dryopteris filix-mas</i>		<i>Veronica chamaedrys</i>	
<i>Eurhynchium praelongum</i>		<i>Mnium hornum</i>	f.
<i>Hylocomium loreum</i>	d.	<i>M. undulatum</i>	a.
<i>Hypnum cupressiforme</i>		<i>Polytrichum juniperinum</i>	
<i>Lophocolea cuspidata</i>		<i>Thuidium tamariscinum</i>	
<i>L. heterophylla</i>			

The ash-oak woods differ from those of the beech in having a more continuous moss carpet, a greater number of species being present and many of these in greater abundance. This has often been attributed to the better light, but the quicker decay of the leaf litter is probably of greater importance. The ground flora under an ash with a beech next to it was no better than under the beech because of the beech litter.

In all these woods, and especially the beechwoods, many plants occur only on or near the "rides", and care has to be exercised in not giving these plants undue importance, since they may be more or less alien to the actual wood.

There is no running water in the combs, and water collects for only a short

<sup>1</sup> Of London Catalogue, 11th ed. (1925).



time in any of the natural depressions. One such depression is known as Shooter's Pond, but it is nearly always without water. There are no exposed rock surfaces, and consequently the great wealth and diversity of rupestral bryophytes and lichens as are found in some oak- and ash-woods are absent. Irregularly shaped chalk stones and rounded flints are sometimes scattered about, and these have a few bryophytes and lichens on them, but the easy disintegration of the chalk and the rolling movements of the flints afford little security of tenure for the development of these plants. On these stones *Seligeria paucifolia*, *Rhizocarpon confervoides*, *Verrucaria mutabilis*, *V. maculiformis*, *V. muralis*, *Thelidium sparsulum* and *Arthopyrenia saxicola* occur in all the woods, but none is frequent except the *Seligeria*.

The beechwoods are remarkably poor in bryophytes and lichens. The slow decay of the leaf litter partly explains the paucity of the moss carpet, but this cannot be the reason for the poor development of the corticolous forms, which are often as poorly represented and as poorly developed as in a wood near an industrial district. The effects of smoke cannot be the cause here, and it seems probable that the thick canopy which excludes a large amount of light is the chief cause of this poverty. In a comparison between these woods and those in the more humid south-west of England the lesser rainfall is a contributory cause of their comparative poverty. The trunks of the beeches in the Cotswolds woods are almost as bare, but farther south and west the beeches found in woods are much better draped with bryophytes and lichens.

The bases of the trees are sometimes clothed with the following species:

*Cladonia fimbriata*  
*C. fimbriata* var. *subulata*  
*C. ochrochlora*  
*C. pyxidata*  
*Eurhynchium myosuroides*

*Eurhynchium myurum*  
*E. praelongum*  
*Hypnum cupressiforme*  
*Lophocolea cuspidata*  
*L. heterophylla* (especially on stray larch)

Occasional species are:

*Atrichum undulatum*  
*Bryum capillare*  
*Eurhynchium abbreviatum* (on beech roots)  
*E. confertum*  
*Mnium cuspidatum*

*Mnium hornum*  
*Plagiochila asplenioides*  
*Plagiothecium denticulatum*  
*Thuidium tamariscinum* (sometimes 2-3 ft. from base)

The higher portions of the trees, which have a less constant water supply, are usually bare, but *Hypnum cupressiforme* (especially its variety *filiforme* and occasionally its variety *resupinatum*), *Pertusaria amara*, *P. communis* and *P. wulfenii* are sometimes abundant.

Frequent species are:

*Frullania dilatata*  
*F. tamarisci*  
*Graphis elegans*  
*G. scripta*  
*Hypogymnia physodes*  
*Lecanora chloroneura*  
*Lecidea parasema*  
*Metzgeria furcata* var. *fruticulosa*  
*Microlejeunea ulicina*

*Neckera complanata*  
*N. pumila*  
*Parmelia caperata*  
*P. revoluta*  
*P. saxatilis*  
*Phlyctis agelaea*  
*P. argenta*  
*Porina carpinea*  
*Pyrenula nitida*  
*Ulota crispa*

The following are occasional:

Arthropryenia epidermidis  
Bacidia phacodes  
Dicranum scoparium  
Enterographa crassa  
Evernia prunastri  
Lecanora conizaeoides  
L. expallens  
Opegrapha betulina  
Orthotrichum affine  
O. lyellii  
Parmelia fuliginosa var. laetevirens  
P. perlata

Parmelia subaurifera  
P. sulcata  
Pertusaria leioplaca  
P. multipuncta  
Phaeographis dendritica  
P. inusta  
Radula complanata  
Usnea ceratina  
U. florida  
U. florida var. hirta  
Zygodon viridissimus

No species of *Ramalina* or corticolous *Acrocordia* or fertile Coniocarpales were seen in the beechwoods. Occasional elders were present but they did not show any *Cryphaea heteromalla* or *Xanthoria parietina* or the wealth of crustaceous lichens which are present on them in many woods. From the rarity of nitrophilous lichens one must conclude that birds are not numerous: in fact the Goodwood estate has been known as the "silent forest". A little *Xanthoria parietina* and *Physcia hispidula* were found in the beech consociation, and *Xanthoria polycarpa* was seen in the scrub, but otherwise coprophilous species were conspicuous by their absence.

The bryophytes on the ground in the actual beechwood, excluding those which are found only on the paths, consist chiefly of:

Brachythecium rutabulum  
Eurhynchium striatum  
Fissidens bryoides  
F. taxifolius

Hylocomium triquetrum  
Hypnum cupressiforme  
Mnium hornum  
Thuidium tamariscinum

Occasional species are:

Amblystegium serpens  
Atrichum undulatum  
Brachythecium purum  
B. velutinum  
Bryum capillare  
B. caespiticium  
Calypogeia fissa  
Campylium chrysophyllum  
Dicranella heteromalla  
Dicranum scoparium  
Eurhynchium abbreviatum  
E. confertum

Eurhynchium piliferum  
E. praelongum  
E. pumilum  
Fissidens viridulus  
Hylocomium loreum  
Lophocolea bidentata  
L. cuspidata  
Mnium rostratum  
M. undulatum  
Plagiochila asplenioides  
Polytrichum formosum

*Eurhynchium piliferum* may become frequent where ash occurs, *Atrichum undulatum* when ash or oak are present, *Hylocomium squarrosum*, which is frequently found on or near paths, may become abundant when conifers are present, and *Porotrichum alopecurum* is often frequent near the ash-oak fringes. A neighbouring ash or oak or a regeneration circle causes *Eurhynchium striatum* and *Atrichum undulatum* to become abundant, and *Polytrichum formosum* becomes abundant where there is considerable leaching. The mossy carpet is very discontinuous in the beech consociation, slightly better in the beech associates, fairly good in the ash-oak associates and still better in the coppice and scrub.

Lichens are practically absent from the ground flora of all the woods. They occasionally occur on the paths or at the margins. In the scrub a few terricolous *Cladoniae* may become frequent, but other ground lichens as *Peltigerae* and *Leptogia* are usually on the paths.

Corticicolous lichens are rare and often badly developed in the beech consociation, the ill-development being chiefly on the more shaded side and particularly noticeable in *Parmelia caperata*. They are rather better developed and more frequent in the ash-oak associates and coppice and are most frequent at the fringes of the woods and in the scrub. No species of *Ramalina* was met with in the beechwood, but some species were plentiful in the scrub where *Parmelia* spp. are well developed and often frequent.

As previously mentioned an attempt was made to differentiate between the bryophytes and lichens of the various seres and stages of the beechwoods, and lists were made in which the frequencies in these subdivisions were given. In sere 1, which has the deeper and more strongly leached soil, there is some tendency for *Polytricha* and the following species to become more frequent:

<i>Amblystegium serpens</i>	<i>Fissidens taxifolius</i>
<i>Calypogeia fissa</i>	<i>Lophocolea heterophylla</i>
<i>Chiloscyphus pallescens</i>	<i>Mnium hornum</i>
<i>Dicranum scoparium</i>	<i>Plagiochila asplenioides</i>
<i>Eucalyx hyalinus</i>	<i>P. asplenioides</i> var. <i>major</i>
<i>Eurhynchium piliferum</i>	

while *Acrocordiae*, *Parmeliae* and the species in the next list are less evident and in some cases absent:

<i>Campyllum chrysophyllum</i>	<i>Microlejeunea ulicina</i>
<i>Eurhynchium myurum</i>	<i>Seligeria paucifolia</i>
<i>E. striatum</i>	<i>Thelidium sparsulum</i>
<i>Evernia prunastri</i>	<i>Thrombium cretaceum</i>
<i>Hypnum molluscum</i>	<i>Verrucaria muralis</i>

In general the more calcareous the soil of the sere or the earlier the stage the more frequent were the bryophytes, but much variation was noticed. Sere 1 of the beech consociation usually has its bryophytes more scattered than seres 2 or 3, but where sere 3 abuts on sere 1 the trees are crowded and the ground vegetation is as poor in the former as in the latter. In sere 2 the *Oxalis* stage was noticed to be more barren of mosses than the bare stage. Better spacing of the trees or the introduction of a conifer or other tree often caused the ground mosses to become more abundant. The differentiation was so slight and so liable to variation that the subdivisions have been discarded in the list given on pp. 146–155.

Besides those given in the list the following bryophytes and lichens were noticed on the Goodwood estate.

In the beech consociation:

<i>Graphis scripta</i> var. <i>pulverulenta</i>	<i>Plagiochila asplenioides</i> var. <i>major</i>
var. <i>recta</i>	<i>Porina lectissima</i> (flints, r.)
var. <i>serpentina</i>	<i>Rhizocarpon viridiatrum</i> (flints, r.)
<i>Leciograpta parasitica</i> (on <i>Pertusaria</i> )	

(Text continued on p. 155).

*List of bryophytes occurring in various beech and related communities  
of Southern England*

*Nomenclature.* The names of bryophytes are generally those given in the *Census Catalogues* (1926, 1930) of the British Bryological Society. The names of lichens are generally those given in the *Monograph of British Lichens* (Smith, 1918 and 1926), except for modifications introduced in the "Classification of lichens" (Watson, 1929).

*Arrangement of the List.* The first eight columns in the list refer to the occurrence of the bryophytes and lichens in the following communities of beech and related vegetation.

(1) Beechwoods on the oolitic rocks of the Cotswold Hills (Oolite—Cotswolds).

(2) Beechwoods on the Chalk Escarpments and valley sides, i.e. on shallow chalk soil (Chalk Escarpment).

Columns 3–7 refer to the vegetation of the Chalk Plateaux.

(3) General list from the beechwoods of the Plateau (General).

(4) Beech consociation.

(5) Beech associates.

(6) Ash-oak associates.

(7) Scrub.

(8) Beechwood on acid Eocene beds (Acidic beds).

The frequency letters are as follows:

d. = dominant	f. = frequent	v.r. = very rare
s.d. = subdominant	o. = occasional	— = not seen and presumably rare or absent
a. = abundant	r. = rare	l. = local

When a space in a column opposite the name of a species is left blank the species was regarded as definitely absent.

The ninth column refers to the particular habitat, of which five are recognised, as follows:

Trunks = tree trunks.

Bases = bases of trees, stumps or other dead wood.

Ground = the soil surface.

Banks = banks.

Stones = rocks or stones.

( ) The enclosure of a habitat in brackets indicates that this habitat is unusual.

The tenth column contains further indications of habitat, and the following abbreviations are used:

Paths = usually on or near paths; border plants.

Paths† = general ground flora of siliceous woods only; in calcareous woods only on paths or other leached soil.

Damp = moist places such as sides of ditches.

Margins = more open places or edges of woods.

Chalk = on scattered chalk stones lying on the soil.

Flints = on flints lying on the soil.

Grass = more frequent on neighbouring grassland.

Conifers = especially abundant on or near conifers.

Parasite = lichens or fungi parasitic on other lichens.

\* = plants which in woods on siliceous soil are often present on soil or rock, but in woods on calcareous soil are rarely present except on tree bases or stumps.

	Oolite —Cots- ment	Chalk Escarp- ment	Chalk Plateaux			Acidic beds	Habitat	Notes
			General	Beech conso- ciation	Ash- Beech oak associes			
Mosses:								
<i>Amblystegium serpens</i>	f.	o.	f.	f.	o.	—	Ground, stones	
<i>A. confervoides</i>	f.	f.	o.	—	—	—	Ground	Damp
<i>A. filicinum</i>	f.	f.	—	—	o.	—	All but trunks	
<i>Anomodon viticulosus</i>	o.	r.-o.	f.	o.	f.-a.	f.	" "	Pathist
<i>Atrichum undulatum</i>	o.	o.	o.	—	—	o.	Ground, banks, stones	Margins
<i>Barbula convoluta</i>	o.	o.	o.	—	—	—	" "	"
var. <i>sardoa</i>	o.	o.	o.	—	—	—	Banks, (stones)	Paths, margins
<i>B. cylindrica</i>	f.	o.	r.	—	—	r.	Banks	
<i>B. fallax</i>	f.	o.	o.	o.	o.	o.	Banks, stones	
<i>B. rubella</i>	f.	o.	o.	o.	o.	o.	Stones	Damp, margins
<i>B. tophacea</i>	l.a.	o.	o.	o.	—	—	Ground, banks, stones	
<i>B. unguiculata</i>	o.	o.	r.-o.	r.	o.	f.	Banks, stones	Margins
<i>Brachythecium glareosum</i>	o.	o.	—	—	—	—	Ground	
<i>B. purum</i>	f.	o.-f.	o.	o.	o.	o.	All but trunks	
<i>B. rutabulum</i>	f.-a.	f.-a.	o.-f.	f.-a.	f.-a.	o.	" "	
<i>B. salebrosum</i>	v.r.	r.	v.r.	—	—	—	All	Margins
<i>B. velutinum</i>	f.	f.	o.-f.	o.-f.	f.	f.	Banks, stones	
<i>Bryum caespitium</i>	o.	o.	o.-f.	o.	—	—	All but trunks	
<i>B. capillare</i>	f.	r.-o.	o.	o.	o.	—	Banks, stones	
<i>B. inclinatum</i>	o.	o.	r.	r.	—	o.	Ground, banks, stones	
<i>B. pendulum</i>	r.	r.	r.	r.	—	o.	Ground, banks	Grass
<i>Camptothecium lutescens</i>	o.	o.	—	—	r.	o.	Trunks, stones	Margins
<i>C. sericeum</i>	f.	o.-f.	r.	o.	—	f.	Ground, banks, stones	
<i>Campyllum chrysophyllum</i>	o.	o.	o.	o.	—	—	Stones, (bases)	*
<i>C. hispidulum</i> var. <i>sommerfeltii</i>	f.	f.	—	—	—	o.	Ground, (bases)	Margins
<i>Campylopus flexuosus</i>	v.r.	—	—	o.-f.	—	o.	Ground, banks	"
<i>Ceratodon purpureus</i>	o.	o.	—	—	—	—	" "	"
<i>Cylindrothecium concinnum</i>	o.	o.	—	o.	—	o.	" "	Margins
<i>Dicranella heteromalla</i>	o.	o.	—	o.	—	—	" "	"
<i>D. schreberi</i>	r.	r.	r.	o.	—	—	Trunks	Margins
<i>Dicranoreisia cirrata</i>	o.	o.	—	r.	—	—	Ground, banks	Grass
<i>Dicranum bonjeani</i>	r.	r.	r.	r.	—	—	Banks	
<i>D. majus</i>	r.	r.	r.	o.	—	f.	All habitats but trunks	
<i>D. scoparium</i>	o.-l.a.	o.-l.a.	o.	o.	f.	o.-f.	Ground	Grass
var. <i>orthophyllum</i>	o.	o.	o.	o.	—	—	Trunks, bases	
<i>D. strictum</i>	r.	r.	—	—	—	—	Trunks, bases	



	Oolite —Cots- wolds	Chalk Plateaux					Acidic beds	Habitat	Notes
		Chalk Escarp- ment	General	Beech conso- ciation	Beech oak associes	Scrub			
<b>Mosses (cont.):</b>									
<i>Hypnum cupressiforme</i>	f.	o.-a.	a.	a.	a.	o.	r.	Trunks	Grass, margins
var. <i>filiforme</i>	o.	r.	o.	o.	—	—	—	Banks, (stones)	Damp, grass
var. <i>resupinatum</i>	r.	r.	r.	r.	—	o.	—	—	—
var. <i>tectorum</i>	f.	r.	r.	r.	—	—	—	Ground	—
<i>H. cuspidatum</i>	a.	f.-a.	r.	r.	r.	r.	f.	Grass, banks, stones	—
<i>H. molluscum</i>	r.	l.	r.	—	r.	r.	—	(Ground, banks	—
<i>H. schreberi</i>							o.-a.	Ground, (bases)	—
<i>Leucobryum glaucum</i>	f.	o.	—	—	—	—	—	Trees, stones	Margins
<i>Leucodon sciuroides</i>	r.	o.	—	—	—	—	—	Ground, banks	—
<i>Mnium affine</i>	r.	r.	o.	o.	o.	o.	a.	Bases, grasses, banks	—
<i>M. cuspidatum</i>	o.	r.	f.	f.	o.-a.	l.f.	—	" "	Pathst†
<i>M. hornum</i>	o.	r.	o.	o.	—	—	—	Banks, stones	Damp, paths
<i>M. punctatum</i>	f.	o.	o.	o.	f.	—	—	" "	—
<i>M. rostratum</i>	f.	o.	o.	o.	—	—	—	Banks, stones	—
<i>M. stellare</i>	o.	r.	—	—	—	—	—	" "	—
<i>M. undulatum</i>	f.	o.-l.f.	o.	o.	f.	a.	—	Ground, banks	—
<i>Neckera complanata</i>	f.	f.	o.	o.	o.	f.	—	Trunks	—
<i>N. crispā</i>	o.	r.	—	—	—	—	—	Stones	—
<i>N. pumila</i>	o.	o.	o.-f.	f.	o.	—	—	Trunks	—
var. <i>philippeana</i>	o.	r.	o.-f.	f.	o.-f.	—	—	" "	—
<i>Orthotrichum affine</i>	o.	o.	o.	o.	o.	o.	—	Stones	Margins
<i>O. anomalum</i> var. <i>saxatile</i>	o.	r.-o.	—	—	—	—	—	Trunks	"
<i>O. cupulatum</i>	o.	o.	—	—	—	—	—	" "	Margins
<i>O. lyelli</i>	o.	o.	—	—	f.	—	—	" "	Margins
<i>O. pulchellum</i>	r.	r.	—	—	—	—	—	Ground	Paths
<i>Physcomitrium pyriforme</i>	—	—	r.	r.	—	—	—	Bases, ground, banks	—
<i>Plagiothecium denticulatum</i>	o.-f.	o.	r.	—	o.	—	—	Ground, stones	—
<i>P. depressum</i>	o.	o.	r.	—	—	—	—	Bases, ground, banks	—
<i>P. sylvaticum</i>	o.	o.	r.	r.	o.	—	—	Ground, banks	—
<i>Polytrichum formosum</i> <sup>1</sup>	o.	r.	o.	l.f.	o.-f.	o.	o.-f.	" "	Pathst†
<i>P. gracile</i>	—	l.r.	l.	l.f.	—	—	—	" "	Pathst†
<i>P. juniperinum</i>	v.r.	—	l.	l.	l.	f.	o.	" "	Pathst†
<i>Porotrichum alopecurum</i>	f.	o.-f.	r.	r.	o.	f.	—	Ground, banks, stones	Margins
<i>Seligeria calcaria</i>	v.r.	f.	—	—	—	—	—	Stones	Margins, chalk
<i>S. paucifolia</i>	f.	r.	o.-f.	o.-f.	f.	f.	—	" "	Chalk

<sup>1</sup> Often present on banks yards away from path.

	Chalk Plateaux					Notes	
	Oolite —Cots- wolds	Chalk Escarp- ment	General	Beech conso- ciation	Ash- oak associ- es		Acidic beds
<b>Mosses (cont.):</b>							
<i>Seligeria pusilla</i>	f.	v.r.	—	—	—	—	Stones
<i>Tetraphis pellucida</i>	v.r.	—	—	—	—	o.	Bases, ground
<i>Thuidium philiberti</i>	r.	r.	—	—	—	—	Ground, banks, stones
<i>T. tamariscinum</i>	f.	o.f.	f.-a.	f.	f.	o.-l.f.	All
<i>Tortula laevipila</i>	f.	f.	o.	o.	—	—	Trunks
<i>T. subulata</i>	f.	f.	o.	o.	—	—	Banks
<i>Trichostomum tortuosum</i>	o.-l.a.	o.	—	—	—	—	Banks, stones
<i>Ulotia bruchii</i>	r.	r.	o.f.	o.	o.	—	Trunks
<i>U. crispa</i>	r.	r.	f.	f.	f.	—	"
var. <i>intermedia</i>	r.	r.	f.	f.	f.	—	"
<i>Webera albicans</i>	r.	r.	r.	r.	r.	—	Ground
<i>W. nutans</i>	v.r.	—	v.r.	—	—	o.	Bases, ground
<i>Weisia microstoma</i>	o.	o.	—	—	o.	—	Ground, banks
<i>W. tenuis</i>	o.	r.	—	—	—	—	Stones
<i>W. verticillata</i>	o.	r.	—	—	—	—	"
<i>W. viridula</i>	o.	o.	o.	o.	o.	—	Ground, banks
<i>Zygodon viridissimus</i>	o.f.	f.	o.	—	—	—	Trunks
<b>HEPATICS:</b>							
<i>Aneura pinguis</i>	o.	o.	o.	—	—	—	Ground
<i>Anthoceros laevis</i>	r.	r.	r.	—	—	—	"
<i>Calypogeia fissca</i>	o.	o.	f.	—	—	—	Ground, banks
<i>C. trichomanis</i>	—	—	—	—	—	o.	Ground
<i>Cephalozia bicuspidata</i>	r.	r.	r.	r.	o.	o.	Bases, ground, banks
<i>Chiloscyphus pallescens</i> <sup>1</sup>	o.	r.	o.	o.	—	—	Ground
<i>Diplophyllum albricans</i>	v.r.	—	—	—	—	o.	All but trunks
<i>Fossombronina caespitiformis</i>	—	—	r.	—	r.	—	Ground
<i>F. wondraczeki</i>	r.	r.	r.	r.	o.	o.	"
<i>Frullania dilatata</i>	f.	f.-a.	o.	o.	f.	o.	Trunks
<i>F. tamarisci</i>	r.	o.	o.	o.	f.	v.r.	"
<i>Lepidozia reptans</i>	l.r.	r.	r.	r.	—	o.	All but trunks
<i>Lophocolea bidentata</i>	f.	o.-f.	o.	o.	o.	o.	Ground, banks, stones
<i>L. cuspidata</i>	a.	f.	f.	f.	f.	—	All but trunks
<i>L. heterophylla</i>	a.	f.	f.	f.	f.	—	"
<i>Lophozia attenuata</i>	r.	r.	r.	—	—	o.	Bases, banks, stones

<sup>1</sup> Often present on banks yards away from path.

<sup>1</sup> Often present on banks yards away from path.



	Oolite —Cots- wolds	Chalk Escarp- ment	Chalk Plateaux				Acidic beds	Habitat	Notes
			General	Beech conso- ciation	Beech oak associates	Scrub			
HEPATICS ( <i>cont.</i> ):									
<i>Lophozia badensis</i>	f.	r.	—	—	—	—	—	Ground	Damp
<i>L. turbinata</i>	f.	o.	—	—	—	—	—	"	"
<i>Lunularia cruciata</i>	o.	o.	o.	o.	—	—	—	Bases, stones	Paths
<i>Madotheca laevigata</i>	o.	r.	—	—	—	—	—	"	Margins
<i>M. platyphylla</i>	f.	f.	f.	—	—	f.	—	Trunks	
<i>Metzgeria furcata</i>	f.	f.	f.	o.-f.	f.	o.	—	"	
var. <i>fruticulosa</i>	o.	o.	o.-f.	f.	o.	—	—	"	
<i>M. pubescens</i>	f.	f.	f.	f.	f.	o.	—	Stones	
<i>Microlejeunea ulicina</i>	r.	r.	f.	f.	—	—	r.	Trunks	Damp, paths
<i>Pellia epiphylla</i>	f.	f.	f.-a.	o.	—	—	—	Ground	"
<i>P. fabroniana</i>	f.	f.	f.	—	—	—	—	"	"
<i>Plagiochila asplenoides</i>	o.-f.	o.-f.	f.	—	—	o.	—	All but trunks	
<i>Radula complanata</i>	o.	o.	o.	—	—	o.	r.	Trunks, (stones)	
<i>Riccia glauca</i>	r.	—	r.	—	r.	—	—	Ground	Paths
<i>Scapania aspera</i>	o.	o.	r.	—	—	—	—	Banks, stones	Margins
LICHENS:									
<i>Acarospora heppii</i>								Stones	Flints
<i>Acrocordia biformis</i>	r.	r.	—	—	—	—	r.	Trunks	
<i>A. epipolaea</i>	r.	r.	r.	r.	r.	r.	—	Stones	Chalk
<i>A. gemmata</i>	r.	r.	—	—	—	—	—	Trunks	
<i>A. monensis</i>	—	r.	r.	r.	r.	r.	—	Stones	
<i>Arthonia gregaria</i>	o.	r.	r.	—	—	o.	—	Trunks	
<i>A. lurida</i>	r.	r.	r.	r.	o.	r.	r.	"	
<i>A. radiata</i>	o.	r.	r.	—	—	o.	o.	"	
var. <i>swartziana</i>	o.	r.	r.	—	f.	f.	o.	"	
<i>Arthopyrenia epidermidis</i>	o.	r.	r.	—	r.	—	r.	"	
<i>A. fallax</i>	r.	r.	r.	r.	r.	o.	—	"	
<i>A. saxicola</i>	r.	r.	r.	r.	r.	r.	—	Stones	Chalk
<i>Bacidia arceutina</i>	o.	o.	o.	—	—	o.	o.	Trunks	
<i>B. atrogrisea</i>	r.	r.	r.	r.	r.	o.	o.	"	Margins
<i>B. effusa</i>	r.	o.	o.	—	—	—	o.	"	
<i>B. phacodes</i>	r.	o.	r.	—	r.	o.	o.	"	
<i>B. rubella</i>	o.	o.	r.	—	r.	o.	o.	"	
<i>Baeomyces rufus</i>			v.r.	v.r.	r.	—	o.	All but trunks	
<i>Biatora flexuosa</i>	r.	r.	r.	—	—	—	o.	Bases	Margins

	Oolite —Cots- wolds	Chalk Plateaux			Acidic beds	Habitat	Notes
		General	Beech conso- ciation	Ash- oak associates			
<i>Lucerns (cont.):</i>							
<i>Biatora granulosa</i>	r.	r.	—	—	f.	Bases, ground	*
<i>B. quercea</i>	o.	r.	—	o.	o.	Trunks, bases	
<i>Biatorina griffithii</i>	r.	r.	—	o.	r.	Trunks	
<i>B. lightfootii</i>	r.	r.	—	—	—	"	
<i>Blimbia naegeli</i>	—	r.	—	—	—	"	
<i>B. sabuletorum</i>	o.	r.	—	—	—	Stones	Margins
<i>Botrydina vulgaris</i>	—	r.	—	o.	o.	Ground	Paths
<i>Buellia myriocarpa</i>	o.	r.	o.	o.	o.	Trunks, bases	
<i>Calicium hyperellum</i>	r.	r.	—	o.	o.	Trunks	
<i>Catinaria grossa</i>	r.	r.	—	—	r.	"	
<i>Chaenotheca melanophaea</i>	r.	r.	—	r.	o.	"	
<i>Cladonia caespiticia</i>	r.	r.	—	r.	r.	Bases, ground, banks	
<i>C. digitata</i>	—	r.	—	r.	o.	"	
<i>C. fimbriata</i>	r.	r.	r.	o.	f.	"	*
<i>C. var. subulata</i>	r.	r.	o.-f.	f.	f.	"	*
<i>C. flabelliformis</i>	r.	r.	—	—	o.	Bases, ground, banks	
<i>C. foliacea</i>	r.	o.	o.	o.	o.	Ground, banks	Margins
<i>C. fureata</i>	—	r.	—	—	f.	"	"
<i>C. macilenta</i>	r.	r.	—	r.	o.	Bases, ground, banks	*
<i>C. ochrochlora</i>	r.	o.	o.	o.	f.	"	
<i>C. parasitica</i>	r.	r.	—	r.	o.	Bases, ground, banks	Margins, *
<i>C. pyxidata</i>	o.	r.	r.	o.	o.	"	"
<i>C. var. chlorophaea</i>	r.	—	—	—	—	Banks	Margins
<i>var. pocilla</i>	o.	r.	—	—	—	"	"
<i>C. rangiformis</i>	o.	o.	—	—	—	Ground, banks	"
<i>C. squamosa</i>	r.	r.	r.	r.	f.	All but trunks	Margins
<i>Collema pulposum</i>	r.	o.	—	—	—	Ground, banks, stones	"
<i>Dermatocarpon hepaticum</i>	r.	r.	—	—	r.	"	"
<i>D. lachneum</i>	r.	r.	—	—	—	"	"
<i>Evernia prunastri</i>	o.	o.	o.	o.	o.	Trunks	"
<i>Graphina anguina</i>	r.	r.	—	—	r.	"	"
<i>Graphis elegans</i>	o.	a.	f.-a.	o.	o.	"	"
<i>var. stellata</i>	r.	o.	o.	o.	o.	"	"
<i>G. scripta</i>	o.	f.	f.	f.	o.	"	"
<i>Gyalacta flotovii</i>	r.	r.	—	—	—	"	"
<i>G. truncigena</i>	v.r.	v.r.	—	v.r.	—	"	"

LICHENS (cont.):	Oolite —Cots- wolds	Chalk Plateaux					Notes
		Chalk Escarp- ment	Beech conso- ciation	Beech associates	Ash- oak scrub	Acidic beds	
<i>Hypogymnia physodes</i>	f.	f.	o.	o.	a.	f.	Trunks, bases
var. <i>tubulosa</i>	f.	—	f.	—	—	—	Trunks
<i>Lecania syringea</i>	f.	f.	f.	—	f.	o.	Trunks, bases
<i>Lecanora allophana</i>	f.	f.	—	—	o.	o.	Trunks
<i>L. atra</i>	o.	o.	—	—	o.	o.	Trunks, stones
<i>L. carpinea</i>	o.	o.	f.	—	—	f.	Trunks
<i>L. chlorona</i>	f.	f.	o.	o.	o.	o.	"
<i>L. conizaeae</i>	o.	o.	o.	o.	—	o.	"
<i>L. conizaeoides</i>	o.	o.	o.	o.	—	f.	"
<i>L. expallens</i>	f.	o.	o.	o.	—	o.	"
<i>L. hageni</i>	o.	o.	—	—	—	—	"
<i>L. intumescens</i>	o.	o.	f.	f.	—	—	"
<i>L. pallida</i>	o.	o.	—	—	o.	f.	"
<i>L. rugosa</i>	f.	f.	f.	f.	o.	f.	"
<i>L. subfusca</i>	f.	f.	f.	f.	f.	f.	"
<i>L. symmicta</i>	f.	f.	o.	o.	—	o.	Trunks, bases
<i>L. varia</i>	f.	f.	f.	f.	f.	o.	Trunks
<i>Lecidea crustulata</i>	f.	f.	f.	—	—	—	Stones
<i>L. parasema</i>	f.	o.	o.	o.	o.	f.	Trunks, bases
var. <i>elaeochroma</i>	o.	o.	o.	o.	f.	o.	"
var. <i>flavens</i>	—	o.	o.	—	—	o.	"
<i>Leptogium lacurum</i>	o.	o.	f.	—	—	—	All
<i>Lobaria pulmonaria</i>	f.	f.	f.	—	—	f.	Trunks
<i>Melanthea gelatinosa</i>	f.	f.	f.	—	—	—	"
<i>Microphiale diluta</i>	f.	f.	f.	—	—	—	"
<i>Mycoporum quercus</i>	f.	f.	f.	f.	—	—	Trunks, bases
<i>Normandina pulchella</i>	f.	f.	f.	—	—	—	Trunks
<i>Ochrolechia tartarea</i>	—	f.	f.	—	—	—	"
var. <i>subtartarea</i>	—	f.	f.	—	—	f.	"
<i>Opegrapha atra</i>	f.	f.	f.	o.	o.	o.	"
<i>O. betulina</i>	f.	f.	f.	—	—	f.	"
<i>O. herpetica</i>	o.	f.	f.	—	—	o.	"
<i>O. varia</i>	f.	f.	f.	—	—	o.	Trunks, bases
<i>Pachyphiale cornea</i>	o.	f.	f.	—	—	o.	"
<i>Parmelia acetabulum</i>	f.	f.	f.	—	—	—	Trunks

Margins, flints

Margins

Conifers

Margins

Margins

	Chalk Plateaux				Notes			
	Oolite —Cots- wolds	General ciation						
		Chalk Escarp- ment	Beech conso- ciation	Ash- oak associes		Scrub		
		f.	f.	f.	f.	Acidic beds	Habitat	
<b>LICHENS (cont.):</b>								
<i>Parmelia caperata</i>	f.	f.	f.	f.	o.	r.	Trunks	
<i>P. dubia</i>	o.	o.	r.	r.	o.	o.	"	
<i>P. fuliginosa</i>	r.	r.	—	—	o.	o.	Bases, stones	
<i>var. laetevirens</i>	f.	f.	f.	f.	f.	o.	Trunks, bases	
<i>P. perlata</i>	o.	o.	o.	o.	o.	r.	Trunks	
<i>var. ciliata</i>	—	o.	o.	o.	—	—	"	
<i>P. revoluta</i>	o.	f.	f.	f.	—	o.	"	
<i>P. saxatilis</i>	f.	o.	o.	o.	a.	o.	Trunks, stones	
<i>P. scortea</i>	r.	r.	r.	—	—	o.	Trunks	
<i>P. subaurifera</i>	o.	o.	o.	o.	f.	—	"	
<i>P. sulcata</i>	o.	o.	o.	o.	o.	r.	"	
<i>P. tillacea</i>	r.	r.	r.	r.	—	—	"	
<i>Peltigera canina</i>	o.	r.	—	—	o.	—	Banks	Paths
<i>P. horizontalis</i>	o.	o.	—	—	—	—	"	"
<i>P. polydactyla</i>	o.	r.	r.	r.	o.	—	"	"
<i>P. rufescens</i>	o.	r.	r.	r.	o.	—	"	"
<i>P. scutata</i>	r.	r.	—	r.	—	—	Trunks	Margins
<i>Pertusaria amara</i>	f.	f.	f.	a.	—	f.	"	
<i>P. coccodes</i>	r.	r.	—	—	—	r.	"	
<i>P. globulifera</i>	r.	r.	—	—	—	o.	"	
<i>P. leioplaca</i>	o.	r.	—	—	—	o.	"	
<i>P. lutescens</i>	o.	o.	o.	o.	—	r.	"	
<i>P. multipuncta</i>	r.	r.	r.	r.	—	—	"	
<i>P. pertusa</i>	f.	f.	f.	f.	f.	o.	"	
<i>P. pustulata</i>	r.	r.	—	—	—	r.	"	
<i>P. velata</i>	r.	r.	—	—	—	o.	"	
<i>P. wulfenii</i>	o.	o.	f.	f.	o.	o.	"	
<i>Petractis clausa</i>	o.	r.	—	—	r.	—	Stones	
<i>Phaeographis dendritica</i>	r.	r.	—	r.	—	r.	Trunks	
<i>P. inusta</i>	r.	o.	—	o.	o.f.	o.	"	
<i>Phlyctis agelaea</i>	o.	o.	f.	f.	o.	o.	"	
<i>P. argena</i>	o.	o.	—	—	—	—	"	
<i>Physcia hispida</i>	r.	r.	—	—	r.	o.	Trunks, bases, stones	Margins
<i>var. tenella</i>	r.	r.	—	—	o.	—	"	"
<i>Platysma glaucum</i>	r.	r.	r.	—	o.	r.	Trunks	"
<i>Porina carpinæ</i>	o.	f.	f.	o.	f.	—	"	"

Paths

"

"

Margins

	Oolite —Cots- wolds	Chalk Escarp- ment	Chalk Plateaux				Acidic beds	Habitat	Notes
			General	Beech conso- ciation	Beech associates	Ash- oak			
LICHENS (cont.):									
<i>Porina chlorotica</i>	f.	f.	f.	—	f.	—	—	Stones	Flints, margins
<i>P. olivacea</i>	f.	f.	f.	—	—	—	—	Trunks	
<i>Psora ostreata</i>	v.f.	—	—	—	—	—	o.	"	
<i>Pyrenula nitida</i>	o.	f.	f.	f.	f.	o.	o.	"	
<i>var. nitidella</i>	f.	f.	f.	f.	—	—	—	"	
<i>Ramalina calicaris</i>	o.	o.	o.	—	—	o.	f.	"	
<i>R. evernioides</i>	f.	f.	f.	—	—	—	—	"	
<i>R. farinacea</i>	o.	o.	o.	—	—	o.	f.	"	
<i>R. fastigiata</i>	o.	o.	o.	—	—	o.	o.	"	
<i>R. fraxinea</i>	o.	o.	o.	—	—	o.	o.	"	
<i>R. pollinaria</i>	f.	f.	f.	—	—	—	—	"	
<i>Rhizocarpon albostrum</i>	f.	f.	f.	—	—	o.	o.	"	Margins
<i>Sphinctrina turbinata</i>	o.	o.	o.	—	—	o.	—	"	
<i>Thelidium sparsulum</i>	o.	o.	o.	o.	o.	f.	—	"	
<i>T. viride</i>	f.	—	—	—	—	—	—	Stones	
<i>Thelotrema lepadinum</i>	—	f.	f.	—	f.	—	—	"	
<i>Thrombium cretaceum</i>	—	—	f.	f.	—	f.	—	Trunks, bases	
<i>Usnea ceratina</i>	f.	f.	o.	f.	f.	f.	o.	Stones	Chalk
<i>var. incurvescens</i>	—	—	f.	f.	—	—	—	Trunks	
<i>U. florida</i>	f.	o.	o.	f.	o.	o.	—	"	
<i>var. hirta</i>	f.	o.	o.	f.	o.	o.	—	"	
<i>Verrucaria maculiformis</i>	f.	o.	o.	o.	o.	o.	—	"	
<i>V. muralis</i>	f.	f.	o.	o.	o.	o.	—	Stones	Margins, flints
<i>var. submuralis</i>	—	f.	o.	o.	o.	—	—	"	"
<i>V. mutabilis</i>	f.	o.	o.	o.	o.	o.	—	"	"
<i>Xanthoria parietina</i>	f.	f.	f.	f.	—	o.	f.	Trunks, stones	" , flints

## On the paths or near them:

*Barbula fallax* var. *brevifolia*  
*Bryum atropurpureum*  
*Eucalyx hyalinus*

*Pleurodium subulatum*  
*Polytrichum aloides*

## In the beech associates:

*Pertusaria leptospora* (beech trunk, r.)  
*Verrucaria nigrescens* (flints, r.)

*Verrucaria viridula* (flints, r.)

## On the paths or near them (all rare and incidental):

*Amblystegium juratzkanum*  
*Bryum argenteum*  
*Campylium riparium* (damp place)

*Phascum cuspidatum*  
*Physcomitrium pyriforme*  
*Plagiothecium elegans*

## In the ash-oak associates:

*Arthonia didyma*  
*Lejeunea cavifolia*

*Leptogium sinuatum* (paths)  
*Pottia recta* (paths)

## In the scrub associates:

*Arthonia aspera*  
*Barbula hornschiuchiana*  
*Cephalozia starkii*  
*Cladonia crispata* l.f.  
*Diploicia canescens* o.  
*Lophozia excisa*  
*Peltigera spuria*

*Polytrichum aloides* f.  
*Riccia sorocarpa* (paths)  
*Scapania curta*  
*S. irrigua*  
*Usnea sorediifera*  
*Verrucaria rupestris*  
*Xanthoria polycarpa*

In the coppice the ground was almost covered with *Mercurialis*. The chief mosses were:

*Eurhynchium piliferum* o.  
*Eurhynchium striatum* d.  
*Fissidens taxifolius* a.  
*Hylocomium triquetrum* a.

*Mnium undulatum* f.  
*Porotrichum alopecurum* f.  
*Thuidium tamariscinum* a.

On a path near the beech associates the following hepatics which were not seen, or were very rare, elsewhere were noted:

*Eucalyx hyalinus*  
*Fossombronina pusilla*  
*Lophozia ventricosa*

*Reboulia hemisphaerica*  
*Scapania curta*  
*S. irrigua*

*Algae and fungi of the beech association.* The algae were not particularly noticed. *Vaucheria sessilis* and *V. hamata* were often seen on the paths, *Protococcus viridis* (*Pleurococcus vulgaris*) was, as usual, frequent on the tree trunks, and *Trentepohlia aurea* on the bark and stones. During the investigation of the woods in April and August there was little opportunity for noting the fungi, especially as the August inspection was after a long period of drought. A Mycological Foray of the British Mycological Society on September 22, 1932, yielded some interesting results for the beech consociation, though the day was unfortunately a wet one. All the species of Hymenocycetes in the following list were on the ground (or leaf-mould) unless otherwise noted. The abbreviations are as in previous lists. The nomenclature is after *British Basidiomycetes* (1922) and the lists given in the *Transactions of the British Mycological Society* (1933). Some of the fungi given are not usual

for woods but were on the paths or in more open places, e.g. *Hygrophorus conicus* occurred on a "ride" in the wood.

- Amanita muscarius*  
*A. phalloides* (also in beech associates)  
*A. rubescens*  
*Armillaria mucida* (o., often a. on beech branches)  
*Astroporina scabella*  
*Auricularia auriculae-judae*  
*A. mesenterica*  
*Boletus edulis*  
*Chlorosplenium aeruginosum* (f. on wood in all the woods)  
*Clavaria cinerea*  
*C. cristata*  
*C. kunzei* (paths)  
*C. pistillaris*  
*Collybia fusipes* (wood)  
*C. radicata*  
*Cordyceps militaris* (path in ash-oak associates)  
*Corticium botryosum* (wood, etc.)  
*C. porosum* (fallen twigs)  
*Cortinarius collinitus* (conifer)  
*Craterellus cornucopoides*  
*Crepidotus mollis* (wood)  
*Dacromyces deliquescens* (logs, beech associates)  
*Dichaena faginea* (a., beech associates and conifer)  
*Eccilia griseorubella* (conifer)  
*Entoloma nidorosum*  
*E. rhodopolium*  
*E. sericeum* (margins)  
*Exidia glandulosa* (a., laid logs)  
*Fomes annosus* (conifer stumps)  
*Galactinia succosa*  
*Ganoderma applanatum* (trees)  
*Geaster fimbriatus*  
*Hebeloma crustuliniforme*  
*Hygrophorus ceraceus* (margins)  
*H. chrysodon*  
*H. conicus* (margins)  
*H. psittacinum* (margins)  
*Hypholoma appendiculatum* (wood)  
*H. leucotephrum*  
*Hysterium angustatum* (f., bark in all woods)  
*Illosporium roseum* (on *Pertusaria*, beech associates)  
*Inocybe corydalina*  
*I. descissa* (conifer)  
*I. geophylla*  
*I. pyriodora*  
*I. rimosa*  
*Laccaria tortilis*  
*Lactarius flavidus*  
*L. fuliginosus*  
*L. piperatus*  
*L. pyrogalus*  
*L. quietus*  
*L. serifluus* (damp)  
*L. torminosus*  
*L. vellereus*  
*Lepiota clypeolaria*  
*L. cristata*  
*L. procera*  
*L. sistrata*  
*Leptonia serrulata*  
*Leptopodia elastica*  
*Lycoperdon caelatum* (margins)  
*L. pyriforme* (margins)  
*Macropodia macropus*  
*Marasmius alliaceus* (wood)  
*M. dryophilus*  
*M. globularis*  
*M. hariolorum*  
*M. ramealis* (margins, twigs, etc.)  
*Mycena crocata*  
*M. galericulata* (wood)  
*M. galopus* and var. *nigra* (wood)  
*M. lactea* (conifers)  
*M. pelianthina*  
*M. polygramma* (wood)  
*M. sanguinolenta* (conifers)  
*Myriangium duriae* (trees, beech associates)  
*Omphalaria fibula*  
*Panus stypticus* (wood)  
*Peniophora hydnoidea* (fallen wood)  
*Pleurotus ostreatus* (stumps, etc.)  
*Pluteus cervinus* (wood)  
*P. nanus* (fallen twigs, etc.)  
*Polyporus caesius* (conifers)  
*Polystictus versicolor* (logs in beech associates)  
*Psalliota xanthoderma* (margins)  
*Rhytisma acerinum* (a., on sycamore in beech associates)  
*Russula alutacea*  
*R. chloroides*  
*R. consobrina* var. *sororia* (conifer)  
*R. cyanoxantha* (margins)  
*R. drimeia* (conifer)  
*R. emetica*  
*R. fragilis*  
*R. nigricans*  
*R. puellaris*  
*R. xerampelina*  
*Sebacina incrustans*  
*Tremella mesenterica* (logs, beech associates)  
*Tricholoma argyraceum*  
*T. fulvum*  
*T. grammopodium*  
*T. melaleucum*  
*T. rutilans* (conifers)  
*T. sejunctum* (conifers)  
*T. sulphureum*  
*T. terreum*  
*Ustulina vulgaris*  
*Xenodocheus carbonarius*

A general account of the fungi of beechwoods is given in Watt and Tansley (1932). Many of the species mentioned there were not noted in the beech consociation, partly owing to the little time available for examination and partly because some of them are more frequent in the acidic beech woods.

*Beechwoods on chalk*

The beechwoods of Ditcham Park, Hampshire, were investigated by Adamson (1921) who gave some general notes on the occurrence of bryophytes and included a number of them in his lists. So far as one can estimate from a short visit to the woods his lists give a fair idea of the bryophytic flora though they include some bryophytes which are more characteristic of the fringes of the wood than of the actual wood itself. Any frequent occurrence in the beechwood of such species as: *Seligeria calcarea*, *Camptothecium lutescens*, *Brachythecium glareosum*, *B. salebrosum*, *Orthotrichum anomalum* var. *saxatile*, *Barbula fallax*, *B. unguiculata*, *Polytrichum gracile* and even of *Anomodon viticulosus* or *Camptothecium sericeum* is incidental rather than characteristic. Most of them have xerophytic devices which enable them to live in exposed and dry situations (Watson, 1914). The leaves of *Barbula fallax* are more or less twisted when dry and the cells are small and papillose, whilst those of *B. unguiculata* are closely imbricated and twisted when dry. *Orthotrichum anomalum* var. *saxatile* has a cushion-forming habit, the leaves are closely imbricated and have recurved margins. *Anomodon viticulosus* has its leaves crisped and incurved when dry and the cells are small. *Brachythecium glareosum* has crowded and plicate leaves with twisted apical points. *Camptothecium sericeum*, though it certainly occurs in woods, has densely crowded twisted shoots with closely appressed and plicate leaves with recurved margins and narrow cells, whilst *C. lutescens* (usually on calcareous grassland) is similar though the branches are less tortuose and the leaves less appressed. There is, however, some excuse for the inclusion of these border plants. Some of the calcicolous species of the Downs become much more evident and luxuriant near the margins of the woods and occasionally are found some distance within. Some, which are occasionally found, are included in the general list on pp. 145-9, but others of very rare occurrence are omitted.

There is some doubt about the records of *Seligeria calcarea*, *Dicranum montanum*, *Orthotrichum pulchellum* and *Brachythecium salebrosum*. *Seligeria calcarea* usually occurs in chalk pits in the open, and the plant so recorded was probably *S. paucifolia* which is frequent on scattered chalk stones in Ditcham Park. *Dicranum montanum* is not otherwise recorded for Hampshire, is absent on the Cotswolds and on the Chalk of the Sussex Downs. *Orthotrichum pulchellum* is not otherwise recorded for Hampshire, but is possible as it occurs in Sussex and on the Cotswolds. *Brachythecium salebrosum* is not known to occur in Hampshire, is absent from the woods of the Sussex Chalk, very rarely occurs in the Cotswolds woods, and the plant so recorded is possibly correct but is more probably a form of the variable *B. rutabulum*. In addition to those given in the general list Mr Nicholson of Lewes, who has kindly given me his valuable help, reports the occasional occurrence of *Zygodon conoideus* and *Eurhynchium striatulum* on the Chalk of the Sussex Downs.



No lichens are recorded for the woods though a few are added in subsequent papers of the same series (Tansley and Adamson, 1925, 1926). The following bryophytes tend to become more frequent in the beechwoods of the Chalk as compared with those of the Chalk Plateaux:

Amblystegium filicinum (damp)	Hypnum cuspidatum (damp, sometimes in dry places)
Anomodon viticulosus	H. molluscum
Barbula cylindrica	H. schreberi
Brachythecium glareosum	H. stellatum (damp, margins)
B. purum	Lophozia badensis (damp)
B. velutinum	L. turbinata (damp)
Camptothecium lutescens (margins)	Madotheca laevigata
C. sericeum (margins)	M. platyphylla
Campyllum chrysophyllum	Mnium affine
C. hispidulum var. sommerfeltii	M. rostratum
Cylindrothecium concinnum	M. stellare
Ditrichum flexicaule	Neckera crispa
Encalyta streptocarpa (margins)	Orthotrichum anomalum var. saxatile (margins)
E. vulgaris (margins)	Pellia fabbronia
Eurhynchium confertum	Plagiothecium denticulatum
E. crassinervium	P. depressum
E. murale	P. silvaticum
E. pumilum	Porotrichum alopecurum
E. striatulum	Scapania aspera
E. swartzii	Seligeria paucifolia
E. tenellum	Thuidium philiberti
Fissidens decipiens	Tortula subulata
F. incurvus	Trichostomum tortuosum
Grimmia apocarpa (margins)	Weisia tenuis
G. pulvinata	W. verticillata (damp)
Hylocomium brevirostre	

The following are less frequent or absent:

Atrichum undulatum	Hylocomium loreum
Dicranella heteromalla	Lepidozia reptans
Dicranum majus	Mnium hornum
Diplophyllum albicans	Pellia epiphylla
Eucalyx hyalinus	Polytricha

The corticicolous lichens are not much different. There is a tendency for greater frequency in the terricolous or saxicolous species of *Peltigera*, *Collema*, *Leptogium*, *Dermatocarpon*, *Verrucaria* and *Acrocordia* found on the paths or on scattered chalk stones or near the margins of the woods, but few of them are plants of the actual wood. *Cladonias* and *Baeomyces rufus* are relatively less frequent and rarely occur except on stumps or at the bases of trees. *Cladonia pyxidata* var. *pocilla* and *C. rangiformis* occur on the ground but only in open places or on the outskirts of the wood. Adamson (1921) also describes calcicolous coppice, *Cornus scrub*, oak-hazel (coppiced) wood, and scrub at Ditcham Park. The bryophytes of the oak-hazel wood as he lists them bear a striking resemblance to those of the ash-oak and coppice woods of the Goodwood estate. *Pylaisia polyantha* and *Lophocolea alata* are not otherwise recorded for Hampshire and the *Calypogeia* recorded is more probably *C. fissa* rather than *C. trichomanis*. The bryophytes of the calcicolous coppice are similar to those of the beechwoods of the Chalk except that more light-demanding plants are present. *Lophozia attenuata* is an unusual plant for this

habitat. The bryophytes of the scrub are similar to those of the scrub associates of the Sussex Downs though more calcicolous plants of the margins are present.

*Beechwoods on oolite*

On the northern part of the Cotswolds beech is plentiful in the woods, but many ash, oak and other trees are intermixed. The more pure beechwoods extend southwards from Cheltenham through Stroud to Dursley and Wotton-under-Edge. They are mostly on the escarpment and contain a large number of young beeches on which the epiphytic mantle is poor. A fair number of old beeches are present in Chedworth Wood and in Oakley Park near Cirencester, and these have a better clothing of bryophytes and lichens than the young trees. The poverty of the epiphytic mantle on the Cotswolds is not restricted to the beech: on other trees, which are intermixed, it is relatively poor as compared with that of the more humid woods of the south-west. In the woods of the escarpment it is much poorer than in the more sheltered woods of valleys.

I am indebted to Mr H. H. Knight who conducted me over the area and gave me a great deal of information on the distribution of both bryophytes and lichens. The frequencies of these are given in the general list, which shows that there is much similarity between those found on the Chalk and those on the Oolite. The following are not given in the general list but are found on the Cotswolds: *Barbula ruralis* (o., margins), *Tortula intermedia* (f., margins), *Trichostomum mutabile* (r.), *Brachythecium populeum* (o.), *Amblystegium irriguum* (r., damp), *Campylium stellare* var. *protensum* (o., margins), *Gyalecta cupularis* (o., margins). *Solorina saccata* occurs in some quantity in a limited area in a wood near Stroud along with *Bartramia oederi* and *Lophozia muelleri*, but these three plants have been found nowhere else on the Cotswolds.

*Beechwoods on podsol*

Many of the beechwoods in the London area show much greater acidity than those of the Plateaux (Watt and Tansley, 1932). *Leucobryum glaucum* is an abundant constituent of the moss stratum, and even *Sphagnum* occurs in open places. The bryophytes and lichens are few, but this poverty is probably due to the smoke from the London area, as many plants, which are now absent, have been recorded formerly. The trees have a very scanty covering of mosses or lichens: in fact some of the plants usually found on the trunk were only present on the tree bases or on the beech roots. Even those marked on the list as having the habitat "trunks" were much nearer to the base than usual. The absence of any species of *Fissidens* was remarkable. The age of the beeches, the encroachment of oak, birch, etc., and the abnormal character of the moss stratum suggest that the acidity has increased and that the beechwood is in a degenerate stage though "local but progressive colonisation" is stated to

occur (Watt and Tansley, 1932). At Burnham Beeches the following bryophytes and lichens were noted:

<i>Baeomyces rufus</i>	r.	<i>Hypogymnia physodes</i>	f.
<i>Biatora flexuosa</i>	o.	<i>Lecanora chlorona</i>	f.
<i>B. granulosa</i>	f.	<i>L. conizaeoides</i>	o.
<i>B. uliginosa</i>	o.	<i>L. expallens</i>	f.
<i>Buellia myriocarpa</i>	r.	<i>L. subfusca</i>	r.
<i>Campylopus flexuosus</i>	o.	<i>L. varia</i>	o.
<i>Cephalozia bicuspidata</i>	o.	<i>Lepidozia reptans</i>	o.
<i>Chaenotheca melanophaea</i>	r.	<i>Leucobryum glaucum</i>	a.
<i>Cladina sylvatica</i> var. <i>pumila</i>	o.	<i>Lophozia attenuata</i>	o.
<i>Cladonia digitata</i>	r.	<i>Microlejeunea ulicina</i>	r.
<i>C. fimbriata</i>	f.	<i>Mnium hornum</i>	a.
<i>C. fimbriata</i> var. <i>subulata</i>	f.	<i>Parmelia caperata</i>	o.
<i>C. floerkeana</i> var. <i>carcata</i>	o.	<i>P. dubia</i>	o.
<i>C. furcata</i>	f.	<i>P. fuliginosa</i> var. <i>laetovirens</i>	o.-f.
<i>C. furcata</i> var. <i>pinnata</i>	f.	<i>P. revoluta</i>	o.
<i>C. macilenta</i>	o.	<i>P. revoluta</i> var. <i>rugosa</i>	o.
<i>C. ochrochlora</i>	f.	<i>P. saxatilis</i>	o.
<i>C. pyxidata</i>	r.	<i>P. sulcata</i>	f.
<i>C. squamosa</i>	f.	<i>Pertusaria amara</i>	f.
<i>Dicranella heteromalla</i>	o.	<i>P. pertusa</i>	o.
<i>Dicranoweisia cirrata</i>	o.	<i>P. wulfenii</i>	o.
<i>Dicranum scoparium</i>	o.-f.	<i>Phlyctis argena</i>	o.
<i>Diplophyllum albicans</i>	o.	<i>Polytrichum formosum</i>	o.
<i>Eurhynchium praelongum</i>	o.	<i>Psora ostreata</i>	r.
<i>Evernia prunastri</i>	o.	<i>Tetraphis pellucida</i>	o.
<i>Graphis elegans</i>	o.	<i>Xanthoria parietina</i>	r.
<i>G. scripta</i>	o.	<i>Zygodon forsteri</i>	r.
<i>Hypnum cupressiforme</i>	a.		

In the general list the frequencies of many other plants are given from other sources and observations on similar woods. Some of the plants, such as those given below, are more characteristic of damp heath:

<i>Baeomyces rufus</i>	<i>Diplophyllum albicans</i>
<i>Biatora granulosa</i>	<i>Hypnum cupressiforme</i> var. <i>ericetorum</i>
<i>B. uliginosa</i>	<i>Lepidozia reptans</i>
<i>Botrydina vulgaris</i>	<i>Leucobryum glaucum</i>
<i>Cephalozia bicuspidata</i>	<i>Polytrichum juniperinum</i>
<i>Ceratodon purpureus</i>	<i>Cladonia spp.</i>
<i>Cladina sylvatica</i>	

Some woods in which beech is present in abundance, but which I should hesitate to call beechwoods, are present on some parts of the Chalk Plateaux of the Chilterns and Savernake, also on the Upper Greensand near Chard; and these have a moss flora somewhat intermediate between those of the beechwoods of the Chalk and of the Eocene Basin. They, however, do not contain the heath plants of the latter.

#### REFERENCES

- Adamson, R. S.** "The woodlands of Ditcham Park." *This JOURN.* **9**, 2, 1921 (published in 1922).  
**Armitage, E.** "Vegetation of the Wye Gorge at Symonds Yat." *This JOURN.* **2**, 2, 1914.  
**British Bryological Society.** *Census Catalogue of British Mosses*, 1926.  
**British Bryological Society.** *Census Catalogue of British Hepatics*, 1930.  
**British Mycological Society.** "The Haslemere Foray." *Trans. Brit. Mycol. Soc.* **18**, 1, 1933.  
**Dixon, H. N.** *The Student's Handbook of British Mosses*. 3rd ed., Eastbourne, 1924.  
**Duncan, J. B.** "The mosses and hepatics of Berwickshire and north Northumberland." *Hist. Berwicksh. Nat. Cl.* **25**, 1924.

- Hopkinson, J. W.** "The ecology of the Bunter Sandstone." *This JOURNAL*. **15**, 1, 1927.
- Knight, H. H.** "The mosses of Gloucestershire." *Proc. Cotteswold Nat. Fld Cl.* 1914.
- Leach, W.** "Two relict upland oakwoods." *This JOURNAL*. **13**, 2, 1925.
- Leach, W. and Polunin, N.** "Observations on the vegetation of Finmark." *This JOURNAL*. **20**, 2, 1932.
- Macvicar, S. M.** *The Student's Handbook of British Hepatics*. London, 1912.
- Macvicar, S. M.** "Distribution of hepatics in Scotland." *Trans. Roy. Soc. Edinb.* 1910.
- Mayfield, A.** "Hepatics, mosses and lichens of Suffolk." *J. Ipswich Nat. Hist. Soc.* 1930.
- Paulson, R.** "Lichens of Epping Forest." *Essex Nat.* **17**, 1914; (with **Thompson, P.**) *ibid.* **18**, 1918.
- Rea, Carleton.** *British Basidiomycetes*. Cambridge, 1922.
- Richards, P. W. M.** "Ecological notes on the bryophytes of Middlesex." *This JOURNAL*. **16**, 2, 1928.
- Salisbury, E. J.** "The vegetation of the forest of Wyre." *This JOURNAL*. **13**, 2, 1925.
- Salisbury, E. J.** "The oak-hornbeam woods of Hertfordshire." *This JOURNAL*. **4**, 2, 1916; and **6**, 1, 1918.
- Salisbury, E. J. and Tansley, A. G.** "The Durmast oakwoods near Malvern." *This JOURNAL*. **9**, 1, 1921.
- Smith, A. L.** *Monograph of British Lichens*. Pt. I, 1918; Pt. II, 1926.
- Tansley, A. G. and Adamson, R. S.** "Reconnaissance in the Cotteswolds and the Forest of Dean." *This JOURNAL*. **1**, 2, 1913.
- Tansley, A. G. and Adamson, R. S.** "The Chalk grasslands of the Hampshire-Sussex border." *This JOURNAL*. **13**, 2, 1925.
- Tansley, A. G. and Adamson, R. S.** "The Chalk grasslands of the Sussex Downs." *This JOURNAL*. **14**, 1, 1926.
- Watson, W.** "The bryophytes of the woodlands of Somerset." *New Phytol.* **8**, 3, 1909.
- Watson, W.** "Xerophytic adaptations of bryophytes in relation to habitat." *New Phytol.* **13**, 1914.
- Watson, W.** "Bryophytes and lichens of calcareous soil." *This JOURNAL*. **6**, 1918.
- Watson, W.** "Bryophytes and lichens of fresh water." *This JOURNAL*. **7**, 1919.
- Watson, W.** "The mosses of Somerset." *Proc. Somersetsh. Archaeol. Nat. Hist. Soc.* 1912.
- Watson, W.** "The bogmosses of Somerset." *Proc. Somersetsh. Archaeol. Nat. Hist. Soc.* 1915.
- Watson, W.** "The liverworts of Somerset." *Proc. Somersetsh. Archaeol. Nat. Hist. Soc.* 1920.
- Watson, W.** "The lichens of Somerset." *Proc. Somersetsh. Archaeol. Nat. Hist. Soc.* 1930.
- Watson, W.** "The classification of Lichens." *New Phytol.* **28**, 1929.
- Watt, A. S.** "On the ecology of British beechwoods." *This JOURNAL*. **11**, 1, 1923; **12**, 2, 1924; and **13**, 1, 1925.
- Watt, A. S.** "Preliminary observations on Scottish beechwoods." *This JOURNAL*. **19**, 1 and 2, 1931.
- Watt, A. S. and Tansley, A. G.** "British beechwoods" in **Rübel**, *Die Buchenwälder Europas*, 1932.
- Wheldon, J. A.** "The lichens of Perthshire." *J. Bot. Supp.* 1915.
- Wheldon, J. A. and Wilson, A.** *Flora of West Lancashire*. Eastbourne, 1907.
- Wisniewski, T.** "Les associations des Muscinées épiphytes de la Pologne." *Bull. int. Acad. Cracovie*, 1929.

# SAVANNAH AND FOREST VEGETATION OF THE INTERIOR GUIANA PLATEAU<sup>1</sup>

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(With one Map)

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## I. INTRODUCTION

I FIRST became interested in tropical grass associations because they offered such important alternative and often original hosts to the most serious pests of cane. The present observations were made in the course of journeys in search of new and efficient natural enemies for the cane insects. These journeys took me to large areas seldom or never before visited by a white man and never by an ecologist. It seems therefore worth while to put on record the plant ecological notes, incomplete as they are, in addition to the more purely entomological and economic observations. I have already followed this course in publishing botanical notes on the Venezuelan llanos (Myers, 1933), and the favourable notice of professional botanists has encouraged me to proceed.

The few plants which my main duties and the exigencies of difficult travel allowed me to collect were kindly and promptly determined by Kew and by the U.S. National Herbarium, the grasses especially by Dr A. S. Hitchcock and Mrs A. Chase. All grass identifications in the following pages have been made or, in some few cases, checked by them.

Acknowledgments of the great help received from a large number of people—resident and official—will be found detailed in my official report, now in the press.

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## II. GEOGRAPHICAL AND HISTORICAL

I entered the Rio Branco savannahs in August 1932 from the south, coming up from Manáos, accompanied by Mr Desmond Vesey-FitzGerald as assistant, a very enthusiastic field naturalist, whose observations on the vertebrates and their distribution added greatly to the value of our results. After a considerable stay in the Rupununi savannahs on the British Guiana border, we entered the Pakaraimas, near where the Ireng emerges, and proceeded through this much broken, upland forested country up the left bank of the Ireng, past its head, to the headwaters of the Mazaruni and thence to Roraima, returning to the Rio Branco by the Cotinga-Uraricuera savannahs again in January, *en route* to Georgetown. In June 1933 I entered the Rupununi savannahs again by ascending the Essequibo and Rupununi Rivers, and crossed them to the Rio Branco, *en route* to the Amazon. The return journey was made in December, and that month and January 1934 were spent in exploration of the Rupununi savannahs and adjacent Kanuku mountains and their outliers.

The area of the region in question is not known. We may expect much exact information from the activities of the three Boundary Commissions now and for several years in the field. It is very unfortunate that none of them is accompanied by a naturalist, though Dr A. L. Briceño Rossi, sometime physician to the Venezuelan Commission, made many interesting observations in medical entomology.

*Limits.* The main savannah region is bounded on the north and north-west by the Pakaraima mountains, on the west by the Parima mountains, or rather their foothills, on the south by the great equatorial forest of the Amazon. With this the River Mocaia-i, a large and unexplored tributary of the Rio Branco, forms an exact boundary in the south-west (on the right bank of the Rio Branco), while in the south-east the limits are only imperfectly known. The Guiana forest shuts it off on the east. The Rupununi savannahs are divided into a northern and a southern portion by the wide Kanuku ranges. The limits of the mountain forest areas are indefinite.

*Surface.* The whole of the region lies within the Guianan Forest and Grazing Region of the classification drawn up by Jones (1930, pp. 27-30). From a minimum elevation of about 200 ft. on the Rio Branco it rises to an altitude of about 9000 ft. at the table mountain of Roraima, where meet the frontiers of Venezuela, British Guiana and Brazil. In general it "may be designated a plateau of moderate relief, though deeply seamed in many places by many torrents. The highest lands are tabular, frequently barren, sandstone areas, about which lie extensive crystalline surfaces of irregular relief, here and there capped by volcanics. . . . The sandstone districts have occasioned much of the savannah land in the region, while the soils weathered from the granites, gneisses, and diabase support a usually dense stand of forest" (Jones, *loc. cit.*).

Few stretches are dead level. Most of the country, where not actually mountainous, is undulating.

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*Soils and surface.* The savannah soils vary considerably. There are wide areas of stoneless, soft grey silt, which powders into impalpable white dust, and is eroded curiously into straight-sided blocks, 6 in. to 2 ft. across, sometimes known as terra-wads,<sup>1</sup> with narrow passages between, making most difficult walking, the whole more or less deeply inundated in the wet season. Parts of the bed of the famous Lake Amuku (the site of Raleigh's Eldorado), which is largely a wet-season lagoon, are of this nature in the summer. The higher parts of the savannahs are often largely bare of vegetation and covered with a thick layer of those small ironstone concretions which in Cuba are known as *perdigon* (Bennett and Allison, 1928). Here the giant conical termitaria, up to 12 ft. high and 9 ft. in diameter and often very numerous, form a very striking feature of the landscape, resembling parks of dolmens and cromlechs. Upland savannahs of the Pakaraimas are often strewn with quartz pebbles, with *perdigon*, or with sandstone fragments.

A constant feature of the region as a whole is the alternation of savannah, forest and mountain, which adds perpetual and ever-varying charm to the landscape. Occasionally, on the Uraricuera savannahs, one sees vast level plains, very reminiscent of the llanos, without so much as a bush or a hillock to the horizon. Usually, however, on the most open, level and treeless stretches of savannah, there is always forest in sight, either in the form of fringing woods along one of the numerous rivers, or as bush islands, large or small, while mountains, either the Kanukus, the Pakaraimas or some of the isolated savannah ranges, usually close at least one horizon. The vast forest areas of the Pakaraimas, and even of the Kanukus, are in the same way diversified with occasional small, or even extensive islands of savannah, sometimes on the valley plains and sometimes on the ridges and high plateaux.

On the Brazilian side the sense of freedom and exhilaration experienced by the white man in emerging from the giant equatorial forest into open savannahs is expressed in such place-names as Vista Alegre and Boâ Vista. This feeling is shared in great intensity by the Macusis, who are typical savannah Indians.

*Climate.* At Bom Sucesso, which may be taken as typical of the Rupununi savannahs north of the Kanukus, the rainfall for 1930 was 45.34 in., in 1931 82.01 in., and in 1932 53.67 in. In 1930, which represents a more normal year, there was practically no rain (total 0.25 in.) in October–February inclusive, and well below 2 in. each in September and March. In 1930 rain fell on 97 days, in 1931 on 135 days, and in 1932 on 126 days. At Dadanawa, on the savannahs south of the Kanukus, somewhat drier conditions prevail, the rainfall in 1930 and 1932 being 39.36 in. and 59.10 in. respectively.<sup>2</sup>

<sup>1</sup> A curious term the origin of which is unknown to me. Wallace describes similar savannah surface erosion on the island of Mexiana, at the mouth of the Amazon (*Travels*, p. 68), and a similar phenomenon occurs on the Aripo savannah of Trinidad.

<sup>2</sup> I am indebted for these rainfall records to Father H. Mather, S.J., and to Mr Ashburner.

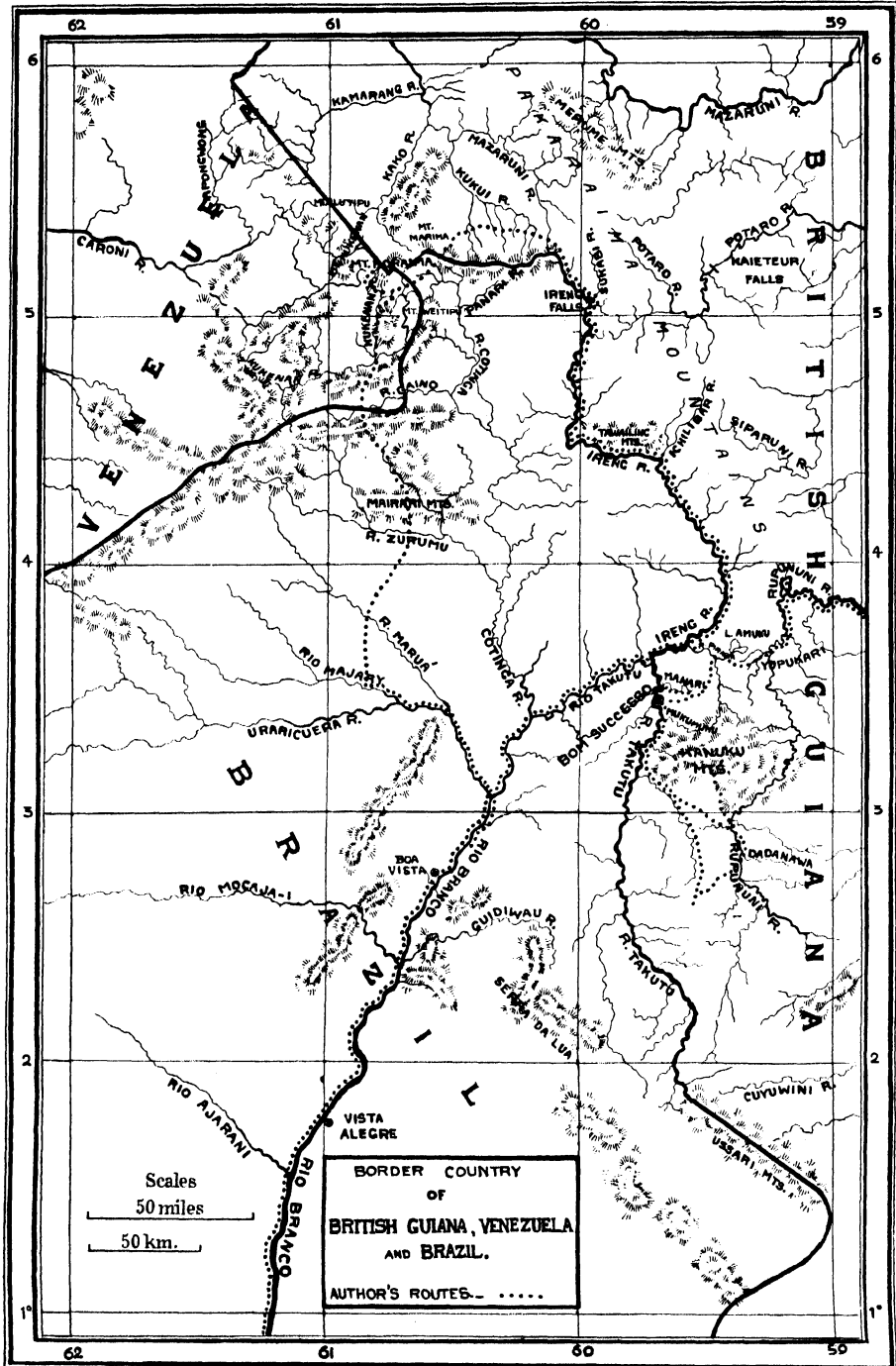


FIG. 1. Sketch map of Border Country of British Guiana, Venezuela and Brazil.



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The lower savannah climate is essentially similar to that of the llanos—a restricted season of heavy rains and a long dry season, leading to the same effects on the vegetation. In the wet season large tracts are under water; in the summer the land is parched for long distances, and even drinking water is hard to procure. The savannah vegetation is thus of climatic origin.

According to Koch-Grünberg (1917, p. 6) there is a periodicity of about 10 years in the climatic cycle of the savannah country. Ordinarily, at least up to the time of his visit in 1911, there is a slight rise in the otherwise falling river in the beginning of December, corresponding with a few days of rain. This rise is known in Portuguese as a *repiquete*, and in *Lingoa geral* as *boiassú* (great snake). About every 10 years this fails.

For the greater part of the region, including the whole of the Pakaraimas and Kanuku mountains, with their forests and savannahs, we have no meteorological data at all, if we except the occasional records of travellers. We know that at the summit of Mt Roraima (9000 ft.) the temperature may drop, at night, to 35° F. It is apparent also that the rainfall of some of the mountain and forest areas is very high. The only indication of the climate as a whole is that afforded by the vegetation.

### III. THE RUPUNUNI-RIO BRANCO SAVANNAHS

*Population and industry.* Save for a very few wandering gold and diamond prospectors, this is the only part of the region which is even approximately settled by any but aboriginal Indians. The British Rupununi savannahs support some ten ranching or mission establishments peopled by whites, and considerably fewer in the hands of coloured people. The Brazilian savannahs carry, in comparison, a considerable white population with one settlement, Boá Vista, of about 1600 people. The three main tribes of savannah Indians are the Wapisianas, Macusis and Taulipang.<sup>1</sup> Practically the only savannah industry is stock-raising (cattle and horses), though the export of skins, especially those of capybara and peccary, is increasing on the Brazilian side. Balata-bleeding (*Mimusops*), gold and diamond washing are extractive industries in the forested portions, within reasonable reach of river transport. Transport difficulty is the great economic obstacle. The natural outlet is down the Rio Branco to Manáos, an easy, deep-water route in the wet season, but the whole of the Brazilian side shares in the economic depression of the Amazon. On the British side the standard route runs down the Essequibo River, with its numerous and highly dangerous rapids, which effectually debar heavy transport. A cattle trail has been opened through the forest to the Berbice, but feeding difficulties for savannah-bred cattle *en route* are great.

<sup>1</sup> The Taulipang are the Arekuna or Arecuna of all visitors to Roraima from Schomburgk onwards. They are invariably called Jaricuna by the Brazilian settlers. The true Arecuna, as Koch-Grünberg has shown, are a tribe of forest Indians inhabiting the unexplored country north of Roraima, about the head of the Caroni.

The cattle industry of the Rupununi began only in the early nineties, but Schomburgk nearly 100 years ago found half-wild cattle which had wandered over from Brazil, where cattle were introduced on the Rio Branco as early as 1796. The effects of stocking on the British (Rupununi) savannahs are at present negligible. The whole area is greatly understocked. Only near ranch buildings and corrals is the effect of local concentrations of stock remarked in the deterioration of pasture shown by pure consociates of inedible weeds like *Sida* spp. On the Brazilian side these areas of *Sida*, and in wetter areas, of the inedible *Ipomoea crassicaulis*, are much more extensive, but in no sense comparable to the huge deteriorated tracts of the Venezuelan llanos (Myers, 1933, p. 348). We are thus in time to study the primitive vegetation of these beautiful savannahs.

*The general savannah vegetation.* By far the greater proportion of the savannah, both flats and undulations, with the sole notable exception of the more or less isolated depressions or *baixas*, is dominated by one abundant grass, *Trachypogon plumosus*. This is present in three ecologically distinct forms, which are apparently not differentiated sufficiently in structure to warrant separation as named varieties. The first, which on these savannahs is by far the most plentiful, is the typical unmodified form; the second is marked conspicuously, especially *en masse*, by a blue-grey bloom which covers the blades, while the third is densely clothed with whitish hairs, giving a fuzzy appearance to the whole plant, even more so than in *Holcus lanatus*, for example. This woolly variant is more abundant in the upland savannahs, but a hoped for correlation between its incidence and the altitude broke down when we found considerable areas on the lower Uraricuera and lower Takutu. There is more evidence that it is correlated with a higher rainfall. There are also indications, which need experimental confirmation, that it is considerably more palatable to stock than the two other forms of this grass. The Macusi name for *Trachypogon plumosus* is *wan-na*. The awned fruits are a nuisance to both horsemen and pedestrians, from their habit of working through the stoutest clothing to the skin.

Typically then, the savannah presents a blue-grey-green expanse of *Trachypogon*, the tufts of which, varying with locality tremendously in size, height and spacing, conceal more or less effectually, and more especially when in flower, a varying proportion of other plants, of which grasses are the most important. Over the whole savannah, in fact, grasses form not only the dominant species, but by far the greater part of the weight of vegetation, and perhaps 90 per cent. of this (over large areas even more) is *T. plumosus*. The important subsidiary grasses are *Aristida setifolia*, *Axonopus aureus*, *Andropogon angustatus* and *Mesosetum liliiforme*. On the Brazilian savannahs *Paspalum stellatum* occurs too. In drier patches the first or the second may be almost pure dominants, but ordinarily they are scattered among the *Trachypogon* tufts. *Andropogon angustatus*, over large stretches locally, is almost as

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abundant as the *Trachypogon*. It flowers first, very profusely, and then its tall reddish stems and inflorescence mask the *Trachypogon* completely and give the appearance of a pure stand. Of non-gramineous elements probably the most important is *Paepalanthus capillaceus* and perhaps other species of the genus. Its balls or snake-like cylinders of green, hairlike tufts are often largely blackened by fire, which stimulates the grass to flower, as Schomburgk first observed. Very frequent also, over large areas, is a small sedge (*Rhynchospora barbata*) with globose brown heads. Another sedge, *Dichromena ciliata*, is also common.

The Dicotyledonous herbs, while adding an almost insignificant quota to the weight of vegetation, are very diverse botanically and frequently have very beautiful flowers. Tiny, but often large-flowered species of *Mimosa*, *Cassia*, *Clitoria*, *Phaseolus*, *Sida*, *Polygala* may be mentioned. I had to neglect them almost entirely, but they were assiduously collected by Schomburgk, from whose material a large proportion has been named. These are all more or less hidden from view by the *Trachypogon* tufts, between which there are also patches, of varying extent, of entirely bare ground.

Intermediate in habit between this inconspicuous ground herbage and the savannah trees is the frequently abundant *Byrsonima verbascifolia*, whose woody parts are so little in evidence that, with its rosettes of large woolly, mullein-like leaves, it passes for a broad-leaved herb.

We have so far considered only the ground vegetation. Small savannah trees and bushes, of which by far the most frequent is the small tree, *Curatella americana*, are seldom entirely absent. Save in isolated areas, however, they are usually more scattered than in "orchard" formation. Next most abundant to *Curatella* are *Byrsonima crassifolia*, *B. coccolobaefolia*, *Bowdichia virgiloides*, *Plumeria* sp., *Roupala* sp., *Psidium* spp., and cashew (*Anacardium occidentale*). Where these shrubs and small trees are grouped more closely together the showy herb, *Amasonia erecta*, appears and sometimes *Heliconia psittacorum* (in damper spots). Cashew forms regular islands, often on knolls, with an undergrowth of *Sida* sp. These agglomerations of savannah trees are to be distinguished from the bush islands described below, and consisting of non-savannah species, and often large trees. The tallest of the pure savannah trees is the *Plumeria*, which is usually solitary. *Curatella*, *Bowdichia* and the two *Byrsonima* bushes are often heavily swathed with the parasitic liane, *Cassytha americana*, and several mistletoes.

Moister flats, still not as damp as the typical baixas, are frequently covered with a very open association of the vivid green grass, *Sporobolus cubensis*, either pure or mixed with *Paspalum lachneum*. Both these grasses are more plentiful on the upland savannahs of the Pakaraimas.

The bush islands and the landward side of the fringing forest are frequently bordered by a wide and very distinctly zoned pure consociation of *Paspalum anceps*, replaced on the Lower Takutu by a closely related but less erect species unfortunately not flowering at the time of my visit.

With *Trachypogon* and *Curatella* as overwhelming dominants the main savannah vegetation may be designated a *Trachypogon-Curatella* association. This community moves as a whole. The grass and the tree tend very regularly to appear at the same distance from the edge of a *baixa* or the fringe of a river bank.

*The bush islands.* These vary from small patches 20 or 30 yards in diameter to stretches of woods several miles across, always marked off very sharply from the savannah. They consist of a curious kind of forest, difficult to classify, of a dryish type, but less deciduous than the larger leaved monsoon-like forest of the Pakaraima foothills. Its origin is undoubtedly edaphic. This forest is made up of a great mixture of shrubs, small trees and lianes, including a strong representation of Myrtaceae, and many Leguminosae. Melastomaceae are largely, often strikingly, absent. Abundant plants are *Bauhinia* sp. (especially as a fringing bush), *Helicteres baruensis*, *Jacaranda* sp., *Apeiba Tipourbou*, *Centrolobium* sp. (*pau rainha*),<sup>1</sup> *Gouania* sp., *Piper* sp., *Solanum* sp., *Inga* sp., *Cordia tetraphylla*, *Myrcia* sp., *Annona* sp., *Guarea* sp., *Scleria flagellum*, *Arthrostyidium*, sp., *Olyra* sp., and *Acrocomia sclerocarpa*. There are occasional *Philodendron*, *Agave* and tall column cactus (*Cereus*). In moister islands *Genipa americana* is frequent, but never so common as in fringing forest.

A locally common bush, with very showy flowers, in rocky bush islands near the northern foothills of the Kanukus, and in the vicinity of Yupukari, is *Clitoria brachycalyx*, which occurs also on the upper rocky slopes of Shiriri Mountain at an elevation of about 2000 ft.

*Fringing forest.* Only very rarely does open savannah extend right to the bank. Where it does so, the savannah, stretching from the brow of the earth cliff, of varying height according to the season, is usually an entirely treeless *Trachypogon* association, known locally as *campo limpo*, or clean savannah. Whether this points to wind effect inhibiting tree growth, or to some other common factor unfavourable to trees, both on the savannah and at the fringe, is not known. Ordinarily there is a belt of very varying width and composition topping the bank. At its greatest development it consists of woods dominated by fairly tall trees, especially *Copaifera officinalis* and dark, wide domes of *Mimosa Schomburgkii*, with fairly frequent large *Spondias mombin*, *Ceiba pentandra* and *Simaruba amara*. This community resembles monsoon forest, or rather the unclassified deciduous forest of the Pakaraimas, much more than that of the bush islands. It is noteworthy that Pittier regards the fringing forest of the Venezuelan llanos as monsoon forest, though neither here nor there is the rainfall sufficient for Schimper's definition. How far the ground water due to the proximity of the river may be considered to supply the deficiency is a matter of opinion. Common smaller trees of the fringing forest are *Genipa americana*, *Cochlospermum* sp., *Cordia tetraphylla*, *Cassia* sp.,

<sup>1</sup> This is the *Ormosia histiophylla* of Richard Schomburgk's *Travels* (2, 33, 89). It appears to be *Centrolobium paraense*, but the uniform red colour of the wood differs from that ascribed to this species by Huber in the Lower Amazon.

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*Helicteres baruensis*, *H. guazumaefolia*, and *Bauhinia* sp. (the same which occurs in the bush islands). Lianes are nearly always abundant. At the height of the dry season a considerable proportion of the trees and bushes are leafless, though the general aspect of the fringe is green. The ground is covered with crackling dead leaves, and in places, sprawling snake-like stems of *Dieffenbachia* sp., with white-tipped leafless shoots bending upwards.

The jauari palm, *Astrocaryum jauari*, is a common feature, usually in groups close to or in the water, both on the main rivers and bordering small savannah creeks. On the former, with *Cecropia* behind, it often forms a special community. On the Lower Uraricuera the latter fringe forest is often dominated by *Triplaris*.

These taller types of fringing woods give place at times to a mere tangle of low trees, bushes and lianes, or even thickets of bamboo (*Guadua*) and prickly bushes and palms, forming an almost impenetrable wall, the maze of stems coated to a height of several feet with mud from the periodic inundations. Where the fringe extends over a wide zone (up to a mile broad) the tangled forest is often interspersed with ponds and lagoons, in which grow stands of a smaller *Genipa* sp.

Nearer the mountains, especially the Kanukus, with increased rainfall, the semi-deciduous fringing forest gives place, e.g. on the Sourab Creek, flowing down from the north-western horn of the Kanukus, to a wide belt of heavy, luxuriant rain forest, with nearly pure stands of tall purple-heart (*Peltogyne*) alternating in patches with mixed rain forest (containing *Cedrela*) and a heavy undergrowth of cocorite palms (*Maximiliana regia*) and *Ravenala guianensis*. This is fringed on the savannah side, like the Kanuku forests themselves, by scattered trees of *Piptadenia peregrina*, the bark of which is the chief tanning material of the ranchers.

We have so far considered the main vegetation of the fringing zone. Save where majestic trees of *Copaifera*, *Spondias*, *Mimosa schomburgkii* and *Ceiba* rise above their fellows, this is less conspicuous from the boat than is the actual line of bushes growing in or at the water's edge. For very long stretches this consists of water-guava (*Psidium*), either leafless and positively beaded with fruit (August) or covered with vivid green leaves (December). This bush takes the place of the willows (*Salix Humboldtiana*) of the Lower Amazon. Either backing the water-guavas, or reaching itself into the water for miles, is a pure fringe of a very leafy *Inga*, the chief food of the hoatzin (*Opisthocomus hoatzin*) in this region.<sup>1</sup> The *Inga* has not the adaptation shown by the

<sup>1</sup> Elsewhere one of the main foods of this extraordinary bird is the giant water-Aroid, *Montrichardia arborescens*. It is curious that we saw practically none of this plant on the Lower Uraricuera (from the Rio Majary), since Hamilton Rice (1928, p. 126) says "the aningas (*Montrichardia arborescens*) form a riparian selvedge. This last growth persists throughout the Uraricuera from near its mouth to where the Rio Parima enters. . . ." Hamilton Rice was on the Uraricuera eight years before our visit, and it is possible that, in correlation with the climatic cycles already mentioned, the fringe vegetation has changed in that period. In fact the plant is so unmistakable, and so familiar to both observers, that this is the only possible explanation.

leguminous shrub, *Drepanocarpus lunatus*, occupying precisely the same niche in the estuaries of the Guiana rivers. The similar widespreading branches of the *Drepanocarpus*, evidently trained by the tides, rise and fall with the water, being almost entirely floating. The *Inga* branches, on the other hand, are more rigid, and when the river rises they are largely submerged. It appears that they then lose their leaves and put out long streamers of rootlets like Spanish moss. When the waters subside the rootlets dry up and are used as nesting material by birds (*Synallaxis* sp.) and rats (*Oecomys flavicans*) in great abundance, and fresh leaves appear.

In other stretches the *Inga* and guava selvedge is replaced by equally pure shrubbery of grey-green *Croton* sp.; in others again, especially where the banks are higher, and in process of erosion, there is no specialised border between the water and the general fringing forest, or the narrow strip of drying mud left by the falling waters may be colonised by a zone of soft green grass clumps, *Eragrostis glomerata*.<sup>1</sup>

Smaller creeks, where they flow through depressions of the savannah, are margined with rather different vegetation, characterised, as on the wet savannahs of the Orinoco Delta, by a dominance of the shrub *Chrysobalanus pellocarpus*.

*The baixas or depressions.* The deeper of these are occupied by actual lagoons, the level of which is greatly lowered during the dry season. The more permanent of these support typical hydrophytes like water-hyacinths (*Eichhornia* spp.) and water-lilies (*Nymphaea* spp.),<sup>2</sup> and may be bordered by *Thalia geniculata* and *Montrichardia*. The more extensive baixas are vast sedge flats (largely *Cyperus articulatus*, *Eleocharis geniculata*) several miles across, inundated to a depth of a foot or more for perhaps half the year. The determining factor between sedge flat and *Trachypogon* savannah is apparently the duration of flooding. The latter type can endure flooding for a limited time, while the former cannot stand desiccation. The ecotone between sedge flat and *Trachypogon-Curatella* savannah is often dominated by a low sward of a fine-leaved *Paspalum*, almost certainly *P. pulchellum*, but unfortunately not in flower at the time of my visit.

Intermediate baixas, subject to longer flooding than *Trachypogon* can endure, but thoroughly desiccated during the dry season, support a very varied growth of such grasses as *Paspalum millegrana*, *P. plicatulum* (a very stout and luxuriant growth form), *P. densum*, *Sacciolepis* sp. and a few coarse sedges, with a medley of suffruticose herbs (*Jussieuia*, *Labiates*, etc.) and low

<sup>1</sup> This grass, in a pure stand, grows up with astonishing speed as the waters recede. About mid-December, on the Takutu, it formed, about a yard from the water's edge, a low soft green young growth like sprouting oats, a yard or two higher up the bank it was in flower, and a yard higher still it was dry and brown.

<sup>2</sup> *Victoria regia* prefers the lagoons and especially the quiet reaches (side channels, *paraná*s, *igarapés*) of rivers, in the forested regions of Guiana and Amazonia. I have never seen it in savannah lagoons.

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bushes, among which *Aeschynomene laxa* is conspicuous. *Coutoubea spicata*, the notorious tingue,<sup>1</sup> grows here, often abundantly.

On sand-dunes on the Lower Takutu, between the narrow fringing forest and the sedge flats, I have seen a curious association of tall *Paspalum milligrana* clumps mixed with small water-guava (*Psidium* sp.) bushes. This sand is widely inundated in the wet season.

Some of the wetter savannahs near Annai (Rupununi River), where they extend to the water's edge, are fronted by tall stands of *Paspalum arundinaceum*.

*Water grasses.* In very striking contrast to the Lower Amazon and Lower Orinoco, neither the rivers nor the savannah lagoons are bordered by beds of floating grasses. Only on the lower Uraricuera and Upper Rio Branco did we see very rare patches of water-hyacinth (*Eichhornia* spp.) in the streams, with equally small and infrequent mixed or separate beds of the floating grass, *Panicum elephantipes*.

*Aeta swamp.* In the baixas the place of the bush islands is taken by the aeta swamps, dominated by long lines or groves of the exceedingly beautiful aeta palm (*Mauritia flexuosa*). The grasses between and fringing the palms consist frequently of *Andropogon bicornis* and *Panicum laxum*, either often dominant over considerable stretches. *Paspalum anceps* is frequent. The actual water may support a fringe of *Montrichardia arborescens*, edged landward with tall stout *Jussieua*. Growing among the grasses are Melastomes, broad-leaved *Scleria* and *Heliconia psittacorum*. Where aeta groves border the source of a spring, they may pass, on higher and drier land, into more typical bush-island forest, the intervening ecotone often dominated by cocorite palm (*Maximiliana regia*), particularly on stony (*perdigon*) ground; but Melastomes are more abundant than in the bush islands of the open savannah. In fact, when occasional *Ischnosiphon* and *Renealmia* come in, this community closely approaches rain forest.

### IV. THE UPLAND SAVANNAHS OF THE PAKARAIMA MOUNTAINS

Between the Rupununi savannahs and Roraima the Pakaraimas, at least along the left bank of the Ireng, are predominantly forested, with occasional isolated islands of savannah, sometimes only a few acres in extent. At the base of Roraima and on the Brazilian side of the border (on the Cotinga and Uraricuera) savannahs are again dominant.

Fairly typical *Trachypogon* savannah, without, however, its commonly associated tree, *Curatella americana* (which is confined to lower altitudes), extends in places to Roraima and up the slopes of this mountain to an elevation

<sup>1</sup> This is said sometimes to cause heavy mortality among hard-driven, hungry stock which eat it. The symptoms are those of "blowing" rather than poisoning. Sometimes for long stretches, in the dry season, it forms the only juicy green growth encountered by the hungry animals and it is well known that these are conditions conducive to blowing. The subject of tingue "poisoning", however, needs investigating.

of about 6500 ft. Most of the upland savannahs, however, present a very different and varied facies, even when *Trachypogon* is among the dominant species. The second dominant is usually *Paspalum contractum*.

Leaving the Rupununi savannahs and entering the foothills, one is soon struck by the abundance of *Andropogon angustatus*, disputing the dominance of the *Trachypogon* more than it usually does on the plains. Tongues of savannah vegetation thrust up into the valleys between slopes of deciduous forest. The relationship is not regular, however, for some of the hills are forested on the sides, with savannah on the top, or show grassy slopes topped by wooded summits. The first extensive savannah, that of Kurasabai, at no great elevation above those of the Rupununi, shows a much greater variety of grasses and sedges, though *Trachypogon* or *Andropogon angustatum* remain dominant in all the drier portions, the latter growing in places in nearly pure stands. Moister areas support tall dense beds of *Paspalum plicatulum*.

North of Kurasabai occasional tiny forest-girt savannah of an acre or less is just a sea of 7 ft. *Andropogon*, a tall reddish, undetermined species, but usually *Andropogon angustatum* is dominant, with *Hibiscus sulphurea* frequent, as on the llanos. A *Paspalum anceps* zone continues to separate the savannah from the forest.

First at an elevation of about 1000 ft. one encounters rocky mountain savannahs, often on steep slopes, with frequent rock outcrops, and much bare ground. The vegetation is here altogether more scanty, and *Paspalum contractum*, with its sparse foliage and wiry culms, comes in as a dominant, and remains so to Roraima and up its slopes. On the Uraricuera savannahs it descends to a lower elevation—probably 600 ft. or less. These savannahs are still fringed by *Paspalum anceps*. In the open, the only two other plants in any numbers are *Trachypogon plumosus* and *Paepalanthus capillaceus*. At higher elevations still *Paspalum anceps*, in isolated stiff clumps, tends to join them in the open savannah. *Curatella* does not rise much above 1000 ft. on this route, and *Byrsonima crassifolia* continues as the most frequent savannah tree. The aeta palm (*Mauritia flexuosa*) occurs in all suitable spots to an elevation of at least 4000 ft.

At 2000 ft., at the top of the great Pakaraima escarpment, the two overwhelming dominants are *Paspalum contractum* and *Trachypogon plumosus*, the former especially on slopes, with very much *Paepalanthus capillaceus* and scattered tall plants of the sedge *Lagenocarpus rigidus*. On drier flats, *Axonopus aureus* and *Aristida torta* are abundant, while wet depressions are sometimes dominated by *Echinolaena inflexa*. *Byrsonima verbascifolia* is locally frequent among the *Paspalum contractum*, and the main savannah trees are *Byrsonima crassifolia*, *Plumeria* sp., *Bowdichia virgiliodes*, *Roupala* sp., but no *Curatella*. Here first appears in any abundance (it is very rare on the Rupununi savannahs) the curious vivid green *Palicourea rigida*, with low rosettes of large cabbage-like leaves and a stiff raceme of bright orange and yellow flowers.



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Wherever slopes appear *Paspalum contractum* and *Paepalanthus* are sole dominants. Where the rocky, quartz-pebble or perdigon-strewn savannah gives place to a brownish indurated claystone, with no stones for miles, the woolly form of *Trachypogon plumosus* covers large areas with practically pure stands. *Paspalum contractum* is not quite confined to pebbly surfaces, but is much more abundant on them than elsewhere. High plateaux of 2500 ft. or more are virtually treeless, with perhaps one gaunt, isolated *Plumeria* per mile, but close examination shows *Byrsonima crassifolia* abundant, but so stunted as to be lower than the dominant grasses and sedges—*Trachypogon-Aristida-Paspalum contractum-Lagenocarpus-Paepalanthus*. *Thrasya petrosa* is abundant on creek banks.

In more broken country (e.g. Kerikabaru), at the same and higher elevations, the smoother slopes are clothed with *Trachypogon*, *Aristida torta* and *Axonopus aureus*; the rocky portions with *Paspalum contractum*, *Lagenocarpus* and *Paspalum anceps*. Beyond Kerikabaru some of the small isolated savannahs are covered largely with *Thrasya petrosa*. In the wider savannahs it tends to cling to forest margins and the shade of the scattered savannah trees, *Byrsonima crassifolia* and *B. coccolobaefolia*. It grows also on termite (*Syntermes*) mounds.

On one of these upland savannahs, at about 2500 ft., I walked some distance to examine the vegetation round what seemed to be two lakes or lagoons which sparkled in the sun, and which I took for temporary inundations in a savannah depression. To my intense astonishment they proved to be patches of erect, glistening white Bromeliads, growing in swampy soil, with iron-stained bog water about their roots, but not visible save on the spot.

At Ipisiau the route continues through almost uninterrupted forest with occasional tiny patches of leached white sand (*muri*, see Martyn 1931) supporting a sparse bushy "heath" vegetation, until Roraima is in sight only about 25 miles away. There one enters extensive savannahs from 3500 to 4000 ft. in elevation, fringed with *Thrasya petrosa* and *Paspalum anceps*, dominated in the open by *Paspalum contractum*, *Paepalanthus capillaceus*, *Trachypogon plumosus*, and, in moister spots, *Echinolaena inflexa*. Other grasses are *Aristida torta* and *Axonopus aureus*. The surface is stony, strewn either with perdigon or fragments of sandstone. *Byrsonima verbascifolia* is abundant, *Lagenocarpus* scarcer. *Byrsonima crassifolia* is the common savannah small tree.

Near Arobopo (4173 ft.) the same vegetation prevails. Damper spots about springs show *Paspalum hyalinum* and more sedges, especially *Rhynchospora barbata*, which extends, however, into the drier *Trachypogon-Byrsonima verbascifolia* community.

On the higher levels, on the ascent of Roraima, *Paspalum anceps* grows more freely in the open than ever before. Huge tufts of iris-like *Axonopus scoparius* occur near rocky creeks. Between 5000 and 5500 ft. *Trachypogon plumosus* (the common form) is the real dominant, though somewhat obscured

by the fully flowering or slightly “*passé*” *Paspalum contractum* in great abundance. *Lagenocarpus rigidus*, *Axonopus aureus*, *Echinolaena inflexa* and *Paepalanthus capillaceus* are plentiful.

At 6000 ft. a curious twisted, glaucous, aloe-like Bromeliad—*Brocchinia cordylinoidea*—appears, and *Paepalanthus*, which it more or less replaces, has gone. At 6500 ft. this *Brocchinia* is dominant in places and pure grasslands cease. The glorious *Utricularia Humboldtii* appears in bogs, and many other plants which have made these slopes a Mecca for botanists and their vegetation comparatively well known. Of our lower savannah plants, *Rhynchospora barbata*, *Lagenocarpus* and *Paspalum contractum* accompany the *Trachypogon* abundantly to this level.

On the route from Roraima to the Uraricuera, via the Kukenan and Cotinga savannahs, *Trachypogon plumosus* continues dominant. Still at 4000 ft. finer grasses are plentiful on the wide valley flats, notably the bright green *Sporobolus cubensis*—in small, widely spaced tufts with much bare earth between. Sometimes, especially on the edge of these flats, another grass, *Paspalum lachneum*, is intermixed. Along the small, ditch-like savannah creeks are beds of *Heliconia psittacorum*. A line of low downs appears snowy with the woolly tufts of *Paspalum contractum*, growing among thickly scattered perdigon.

In the Kukenan valley, still at about 4000 ft., the distribution of savannah types is very clear-cut and picturesque, since every dominant species lends its own colour to the diversified landscape. There are first the river flats (up to a mile or more wide) of a vivid, pure green with *Sporobolus cubensis*, here intermixed with *Paspalum pectinatum*. Behind these on the lower hills rises the bloom-like greenish grey of the woolly form of *Trachypogon plumosus*, topped on the higher slopes by the yellower green of the normal form associated with *Paepalanthus*, *Aristida*, *Axonopus aureus*, *Paspalum anceps* and *P. contractum*, turning into snowy white on the rockier ridges where *P. contractum* grows alone.

On this route one gains a distinct impression that lowland savannah conditions, with the associated fauna (notably the birds) are encountered at a higher elevation than on the predominantly forested route east of the Ireng. *Curatella americana*, for instance, here appears at about 2000 ft., and one is soon again crossing grasslands of the type described in the previous section.

*Note on the savannahs of the Kanuku mountains.* Small patches of savannah occur at the higher levels (1000–2000 ft.) in the Kanuku mountains. The smaller ones show much bushy growth (especially *Byrsonima* spp.) closer than “orchard” formation. The larger ones are in places pure grassland. In general *Trachypogon plumosus* (the common and the woolly form) is dominant, but in places the main communities, even in the open, are *Paspalum anceps*–*Paepalanthus capillaceus*, *Sporobolus cubensis*–*Paepalanthus*, *Trachypogon*–*Paepalanthus*, and some *Paspalum contractum*. *Palicourea rigida* is frequent.

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The chief trees and bushes are *Curatella americana*, *Byrsonima crassifolia*, *B. coccolobaefolia*, *Plumeria* sp., and *Roupala* sp. There is a striking similarity to savannahs of similar elevation in the Pakaraimas.

### V. INFLUENCE OF MAN AND ANIMALS ON THE SAVANNAH VEGETATION

*Burning.* By far the greater portion of these savannahs, both on the Rio Branco-Rupununi plains and in the mountains, is still in a primitive condition. The main influence of man has taken the form of fire, but it is by no means certain how frequent grass fires were before human intervention. Viosca (1931) has shown that fires not uncommonly start spontaneously. The scattered aboriginal Indians are inveterate burners. It is almost impossible to prevent one's Indian carriers from setting light to the dry grass. They do this to signal their approach and for pure fun. I have never seen in South America a savannah however small or isolated or distant from settlement which did not show signs of more or less frequent burning. The ranchers burn to destroy the roughage and encourage young tender growth for their stock. I have shown elsewhere (Myers, 1934) that, in the savannahs of British Guiana at least, under present conditions of understocking, this practice is clearly innocuous, and almost certainly beneficial, being, in fact, almost the only type of pasture management possible in a primitive cattle industry with practically no fences. In the absence of annual fires, the roughage would accumulate to such an extent as to render accidental fires very much more dangerous and destructive to the vegetation. The main savannah plants, notably *Trachypogon plumosus*, *Paepalanthus capillaceus* and *Curatella americana*, are so eminently adapted to burning, which they almost invariably survive, that we are justified in regarding the present vegetation as a fire climax (subclimax in Clements' terminology).

*Grazing.* Like all the grasslands of South America these savannahs have experienced no grazing, save that of a few small deer and (near water) capybaras, from the time the larger Tertiary Ungulates became extinct till horses and cattle were introduced by the white man. Even on the Rio Branco savannahs, where the cattle industry was introduced in 1796, this later grazing has been neither so extensive, so long continued nor so intensive as on the Venezuelan llanos. The Rupununi savannah vegetation is so far practically unmodified by stocking save in the immediate vicinity of corrals, paddocks and ranch buildings, and under present understocking is likely to continue so. On the more thickly populated parts of the Rio Branco savannahs, on the Lower Takutu and on the Uraricuera, one occasionally sees the *Trachypogon* clumps eaten to the ground.<sup>1</sup> There are also considerable areas of pure *Sida* consociates, and in wetter areas, of *Ipomoea crassicaulis*, but nothing comparable

<sup>1</sup> This happens also in the Rupununi in enclosed paddocks, leaving the wiry culms of *Mesosetum loliiforme* apparently dominant.

to the extent of deteriorated pasture (under *Ipomoea* and under *Hyptis*) on the Venezuelan llanos. The process of deterioration as yet has not gone very far.

The upland savannahs, beyond Ichilibar, are almost all unstocked, but it is probably only a question of time before the Indians, now that the Boundary Commissions have brought them into contact with the whites, will bring in cattle and horses at least to the more extensive grasslands.

*Plant species preferred by cattle.* On the Rupununi savannahs, owing to the prevalent understocking, one sees little sign of grazing, save just about corrals, etc., where the vegetation is already modified, or on recent burns, where the cattle congregate to feed on the fresh green shoots of *Trachypogon plumosus* and other grasses, which are not easy to identify in that stage. On the Uraricuera savannahs one frequently sees clumps of *Trachypogon plumosus* cropped or even eaten down by cattle. Where several forms are present the woolly variety is the most grazed. On the Berbice savannahs Martyn has recorded grazing of *Trachypogon plumosus* and *Axonopus aureus*.

Crossing the Rupununi savannahs I observed closely what plants our pack-bullocks actually ate. This was a good test since one knew more or less how hungry an animal was when it ate a certain plant. The observations were made in January, under unusually dry conditions. On the open *Trachypogon* savannah the favourite plant with all five bullocks was *Byrsonima verbascifolia*. The woody stalk of this is never more than a few inches high, though sometimes 2-3 in. thick, gnarled and twisted, evidently kept down largely by the feeding of stock, perhaps assisted by the frequent grass fires. Where this plant was at all frequent the bullocks just wandered from one to the next, entirely neglecting the grasses in between. Easily second in order of preference were fresh shoots of grass or sedge (almost any species) springing from recent burns. Within this category, so far as any preference could be detected, the grasses *Paspalum anceps*, *Sporobolus cubensis*, and *Paspalum lachneum* are favoured. For example, on one stretch of *Andropogon angustatus* mixed in equal proportions with *Paspalum anceps*, to the virtual exclusion of other plants, the bullocks deliberately selected the latter, though both grasses were equally fresh and green. The next most favoured grass was *Trachypogon plumosus*, which was occasionally eaten even where not burned, but rather old, though still green.

All these were reactions common to all the bullocks. Some showed tastes peculiar to themselves. One, for instance, greedily ate the young shoots of *Byrsonima crassifolia* springing from burnt stumps—going well out of its way to browse them. But the other four bullocks passed these shoots aside, often brushing them with their muzzles, as also, curiously enough, did the first animal after an hour or so.

At some of the accommodation paddocks cleared in the rain forest, through which the cattle trail leads from the interior to the Berbice River, the bullocks, then almost starved, ate ravenously *Heliotropium indicum* and other green weeds, save *Sida* sp., which, although fresh and green, was left severely alone.

On the Berbice savannahs the same bullocks, after a first hungry attack on any and every *Trachypogon* clump, tended to concentrate on the younger shoots of this grass. Two animals, not including the one which ate *Byrsonima crassifolia* on the Rupununi, went out of their way to browse on the large, vivid green leaves of *Palicourea rigida*, without eating the intervening grass. One of these ate no grass during the whole day. A third bullock seized a *Palicourea* flower raceme, but dropped it without eating.

On the Rupununi, horses greedily eat a species of *Indigofera*, which grows plentifully in some of the drier *bairas*, and considerably resembles lucerne in habit.

In considering the feeding preferences of the stock it should be borne in mind that the pastures as a whole are evidently deficient in mineral nutrients, judging by the frequent habit of bone chewing on the part of the cattle.

*Introduced grass communities.* About the houses of ranchers, especially on the Brazilian side, are occasional patches of introduced grasses, notably *Dactyloctenium aegyptium*, *Axonopus compressus*, *Eleusine indica*, *Cynodon dactylon* and *Cenchrus echinatus*. *Panicum maximum* has been established on the cattle trail just where it enters the forest beyond Annai (towards the coast), and is growing luxuriantly. I saw one irrigated pasture of Pará grass (*Panicum barbinode*).

*The influence of birds.* There is some evidence that birds may be in part responsible for the initiation of bush islands.<sup>1</sup> It is a common sight, under a spreading and isolated *Curatella americana* in the open savannah, far from fringing forest or bush islands, to see up to twenty or more seedlings of *Genipa americana*, arising quite evidently from seeds dropped by birds perched in the branches. The pigeon, *Columba rufina* and the small parrot, *Conurus aeruginosus*, both of which widely range the savannahs in parties, frequently perch in these trees, but it is not known whether these are responsible for the sowing. In one case I counted beneath one old *Curatella*, with a trunk 2 ft. thick at its base, no fewer than thirty-six seedlings, 2-3 ft. high, of *Genipa americana*, several of *Byrsonima crassifolia*, a guava (*Psidium* sp.) and two other woody plants. One sees far more cases of seedlings, however, than of tall *Genipas* overtopping the original *Curatella* tree, and in the absence of a larger series of intermediate stages, it must not be assumed that bush islands are initiated in this way. *Genipa americana* is not a typical bush-island element; it is far more characteristic of fringing forest.

*Influence of ants and of termites.* The huge, hard earthen termitaria of *Amitermes excellens* Silv.,<sup>2</sup> which are such conspicuous features of the landscape in many of the drier savannahs of the Rio Branco and Rupununi, are

<sup>1</sup> I recorded (Myers, 1932, p. 260) an analogous case in a Haitian lake, where floating beds of *Luziola spruceana* and other grasses often begin by seedlings which take root on the very numerous floating grebes' nests (*Podilymbus podiceps antillarum*).

<sup>2</sup> Kindly determined by Dr T. A. Snyder.

usually devoid of vegetation, though a small savannah tree may sometimes be incorporated in their structure. When they are abandoned, however, and weathered down almost to ground level, they are frequently covered by *Paspalum anceps*, which otherwise, on these lower savannahs, never occurs in the open but only as a border on the landward side of fringing forest and bush islands. *Casuarina carpinifolia* also grows on these denuded termitaria.

The lower, but very wide dome-shaped mounds of *Syntermes snyderi* offer much better opportunities to special vegetation. Where they rose from a rather moist substratum, as though intentionally lifted above a high water table, I saw them, on the upland savannahs, clothed with a tall, waving growth of *Thrasya petrosa*, *Aristida torta* and other dry savannah grasses, surrounded by a sea of sedges and moisture-loving grasses.

At about 4000 ft., near the Kukenan River, these *Syntermes* mounds are as thickly spaced on some of the valley flats as manure-loads dumped on an English field. Here they bear a very distinct and characteristic vegetation—two species of *Psidium*, two species of tall woody *Solanum*, *Casuarina carpinifolia*, *Paspalum anceps*, several Melastomes, a fleshy herb of unknown family, *Thrasya petrosa*, *Panicum rudgei*, and even tall shrubs of *Genipa americana*, evidently sown by birds. The last six of these are all plants of the fringing forest or its margin, and none grow on the open savannah save, on these upland savannahs only, *Paspalum anceps*. The *Casuarina*, at least in this neighbourhood, seems practically confined to the termite mounds.

The low wide mounds of leaf-cutting ants (*Atta*) on the mountain savannahs tend to support a very conspicuous growth, widely different from that of the surrounding savannah, of a stout woolly *Paspalum* (unfortunately not in flower) and the similarly hairy *Panicum*—*P. rudgei*. The position is complicated by the fact that the *Atta* nest seems sometimes to be based on an old (?) abandoned termite mound (*Syntermes snyderi*) but the induced flora of *Atta* and *Syntermes* mounds is almost identical. In both cases, even in the midst of very pebbly savannah, the mounds are devoid of stones, and their vegetation tends to be much more luxuriant, even if it consists of the same grass species.

In the Berbice savannahs (see appendix, p. 183), Martyn found a very definite succession of vegetation, leading eventually to the formation of bush islands, on insect mounds which he ascribed to leaf-cutting ants (*Atta*). The greater proportion of them, so far as my observations go, are termitaria (*Syntermes*), but until the nesting relationships of these two insects are elucidated (cf. paragraph above), remarks on these low mounds must be taken as applying to both. The beginning of the succession is a slightly richer herbaceous vegetation on the mounds than on the surrounding savannah, followed by woody plants and eventually by islands of bush dominated by the small tree, *Byrsoneima spicata*. In some parts of the Berbice savannahs, where *Curatella americana* does not occur as a general savannah tree, it is frequent on termite

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mounds. Plants common to the mounds of the Berbice and of the interior savannahs include *Casearia carpinifolia* and *Panicum rudgei*.

### VI. FOREST TYPES OF THE PAKARAIMA MOUNTAINS

Owing to the difficulty of identifying tree species in the tropical rain forest—a difficulty almost insuperable to the casual traveller—my notes on forest communities are even less complete than those on savannah vegetation. I have not included my observations on the forests of the Kanuku mountains and its outliers, since these have been visited by a well-qualified botanist, Mr T. A. W. Davis, of the British Guiana Forestry Department, whose report has not yet been published in full.

The more easterly route which I took to Roraima, through the Pakaraima mountains, up the left bank of the Ireng and past the headwaters of the Mazaruni, lies very largely in forest, varying in elevation from 500 to 3000 ft. On this line, which is not the usual route to Roraima, but which was opened by the Boundary Commission, no ecological studies had ever been made, and the best botanical information was still that gathered by Schomburgk nearly 100 years ago. I have therefore less compunction in publishing my incomplete observations. I was able to recognise, in a rather hasty march, the following main forest types:<sup>1</sup>

(1) *Deciduous forest*, below 1000 ft. (all altitudes are approximate only, owing to the difficulty of checking the aneroid so far from any known bases). This extended over the foothills from the southern (Rupununi) base of the range to near I-na Creek. It tends to merge into rain forest as one goes higher and further into the mountains. Typically, however, it is similar to the woods clothing the southern slopes of the Venezuelan Coastal Cordillera (cf. Myers, 1933, p. 339), but is perhaps nearer to true monsoon forest. Characteristic trees and bushes—not always associated in the same areas—are *Cochlospermum* sp., *Helicteres guazumaefolia*, *H. baruensis*, *Centrolobium* sp. (*pau rainha*), *Bursera gummifera*, *Cedrela* sp., *Apeiba tipourbou*, *Acrocomia sclerocarpa*, but very often the dominant tall trees were quite unknown to me. Over large areas in the dry season this forest is almost entirely leafless, the dry fallen yellow leaves forming a thick crackling carpet on the ground, exhaling odours reminiscent of a dry English autumn day. Near creeks and river banks *Mimosa schomburgkii* and *Spondias mombin* enter the community, as in typical fringing forest.

(2) *Peltogyne consociation*. Still well below 1000 ft., this occurs on bare, sandy flood plains between Kurasabai and Karabakú. It forms, over limited areas, one of the purest stands of one tree species that I have ever seen. The tall dominants are *Peltogyne* sp., while the seedlings, the underbrush, saplings and small trees are practically all of this same species.

(3) *Mixed rain forest*. Save as isolated patches in wet creek bottoms, true

<sup>1</sup> The occasional interspersed savannahs have been considered in section IV.

rain forest does not appear before the slopes descending to the Ichilibar savannah, facing the great main southern escarpment of the Pakaraimas, are reached. Though of various types it is not markedly different from the drier kinds of Guiana lowland rain forest. Trees up to 150 ft. high are abundant. This forest occurs at intervals about as far as the great Ataro Falls, merging into type 6, above 2000 ft. At its higher levels it is often separated from the savannahs by a dense fringe of bamboo (*Guadua*).

(4) *Mora forest*. Forest in which a tall *Mora* sp. is dominant first appears as a narrow fringe in especially wide and wet creek bottoms below 1000 ft. At higher levels (1300–2000 ft.) it occurs as a very pure type, very like that of Trinidad (where the dominant is *Mora excelsa*) with an abundance of mora underbrush and saplings, and with *Pentaclethra filamentosa* as the most frequent subsidiary species. The taller trees reach at least 200 ft. Mora forest alternates with “coppice” forest (5) and mixed forest (3) as far as the Ataro River, usually at altitudes intermediate between “coppice” (higher) and mixed forest (lower). Soil differences do not seem to be correlated with this distribution.

(5) “Coppice” forest. Above Ireng Falls, and at an elevation of about 2000 ft., first appears an extraordinary forest characterised by the complete dominance of a tree which, in the absence of flowers or fruit, I ascribe provisionally to the genus *Dicymbe*. The ground is covered with its hard, coriaceous leaves, shaded by its seedlings and saplings in almost pure culture. Lianes and epiphytes are rare. The tree itself shoots up eight or more large trunks from one huge base, often partly rooted and elevated on a high mound. From the base of the trunks themselves springs a regular coppice of young leafy shoots. The average height is less than that of mora. This forest type extends at altitudes of 1500–2000 ft. as far as the Muing Creek, in the Mazaruni system.

(6) *Montane mixed rain forest*. This forest occupies the higher ridges at intervals from above the Ireng Falls to the base of Roraima itself, at elevations of 2000–4000 ft. It is moister and usually less tall than type (3), passing into real cloud forest in some, but not all, of the higher localities (above 2500 ft.) with wet moss cushions, a large *Anthurium* on ground and trunks, and an abundance of filmy ferns.

(7) *Asheroa forest*. “*Asheroa*” is the Patamona name for a tall straight tree with strongly buttressed base and large (8–10 in. long) simple very leathery leaves, which covers as a strong dominant vast flat areas at altitudes varying from 1300 to 3000 ft., from near the source of the Ireng nearly to the Cotinga (Kwating). It appears to be tolerant of altitude but never grows on slopes—only on the intervening valley-flats, even slight alternating ridges being clothed in mixed forest. The wide buttresses nearly always begin as stilts, i.e. the buttress is separated from the base of the trunk. In this type of forest lianes and epiphytes are abundant, the latter especially at higher levels, where the trees open out, and ground and trunks are smothered with innumerable huge



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**Anthuriums.** The Patamonas manufacture a kind of *cashiri* (beer) from the just expanding seed-leaves, which appear thickly beneath the nearly pure stands of the parent trees.

**General remarks.** It will be noticed that no fewer than four of these seven types are in the nature of pure consociations of a single species—a phenomenon usually rare in tropical forests.

In types (6) and (7) walking is painful in the extreme, owing to the snaky tangle of roots which cover the ground to a depth of a foot, and are densely screened by a thick layer of dead leaves.

From the foothills of the range to the upper slopes of Roraima itself there has been considerable devastation from forest fires, probably dating from various drought years. Occasionally one walked for miles through weedy second growth of various ages, including long stretches of *Heliconia bihai* or of bracken. At Roraima itself, the vegetation of which is now comparatively well known, and need not be further mentioned here, the highly specialised, very moist cloud forest which clothed the slopes between the savannahs and the base of the vertical walls (i.e. to an elevation of about 7500 ft.), has been largely destroyed, at least on the accessible side of the mountain, by widespread fires during one of the dry seasons between 1924 and 1926, and has been replaced by a fearful tangle of blackberries (*Rubus* sp.), bracken and a small shrubby Melastome. Tate (1932, p. 236) says the main fire occurred in April 1926, which was a notable drought year, but the Fathers of the Rio Branco Benedictine community informed me that there were extensive fires in two or three previous years.

### VII. SUMMARY

1. The region described includes the savannahs of the Rio Branco and Rupununi Rivers, of Brazil and British Guiana, and the Pakaraima mountains, between these and Mount Roraima in Venezuela.

2. The Rio Branco-Rupununi plains are covered with climatic savannah vegetation.

3. This vegetation is dominated by a *Trachypogon plumosus*-*Curatella americana* association, varied by fringing forest along the streams, by bush islands (on higher areas) and by groves of aëta palms (*Mauritia flexuosa*) in the depressions, in some of which are sedge flats inundated for considerable periods.

4. The upland savannahs of the Pakaraima mountains, from 1000 to 6500 ft., are clothed in more varied vegetation, with *Trachypogon plumosus* generally dominant, but *Paspalum contractum* a close second.

5. All this savannah vegetation seems to correspond to a fire climax.

6. The influence of introduced grazing animals, chiefly cattle and horses, has so far been almost negligible on the Rupununi grasslands, comparatively slight on the Rio Branco savannahs, and non-existent on the upland meadows.

7. *Trachypogon plumosus* is readily eaten by cattle, especially its fresh growth. Other plants eaten are *Byrsonima verbascifolia*, *Paspalum anceps*, *Sporobolus cubensis* and *Paspalum lachneum*.

8. Birds, by dropping seeds of forest plants from the branches of savannah trees, and mound-building ants and termites, by offering optimum growing conditions to forest fringe plants, may be concerned on all these types of savannahs, in the initiation of bush islands.

9. The forests of the Pakaraima mountains, from the savannah foothills to 4000 ft. on Mt Roraima, may be divided into seven main types, one of deciduous woods, two of mixed rain forest and four of rain forest consociations each dominated exclusively by one tree species.

10. Notes additional to those of Martyn are appended on the Berbice savannahs, which show a great general similarity to those of the Rupununi, with a few notable physical and vegetational differences.

#### REFERENCES

- Bennett, H. H. and Allison, R. V. *The soils of Cuba*. Washington, xxiv + 410 pp., 3 maps, 10 figs., 1928.
- Jones, C. F. "Agricultural regions of South America. Instalment VIII." *Econ. Geogr.* **6**, pp. 1-36, figs. 123-151, 1930.
- Koch-Grünberg, T. *Vom Roroima zum Orinoco*. Stuttgart, 5 Bde, 1916-28.
- Martyn, E. B. "A botanical survey of the Rupununi Development Company's ranch at Waranama, Berbice River." *Agric. J. Brit. Guiana*, **4**, 18-25, pls. I, II, 1931.
- Myers, J. G. "The original habitat and hosts of three major sugar-cane pests of tropical America (*Diatraea*, *Castnia* and *Tomaspis*)." *Bull. Ent. Res.* **23**, 257-271, pl. 13, 1932.
- Myers, J. G. "Notes on the vegetation of the Venezuelan llanos." *This JOURNAL*, **21**, 335-349, 1933.
- Myers, J. G. "Observations on a journey from the mouth of the Amazon to Mount Roraima and down the Cattle-Trail to Georgetown." *Agric. J. Brit. Guiana*, **5**, 86-100, 1934.
- Rice, A. Hamilton. "The Rio Branco, Uraricuera and Parima." *Geogr. J.*, Feb. Mar. April, 1928.
- Schomburgk, Richard. *Travels in British Guiana, 1840-1844*. Trans. W. E. Roth, Georgetown, 2 vols., 1922.
- Tate, G. H. H. "Life zones at Mount Roraima." *Ecology*, **13**, 235-57, 12 figs., 1932.
- Viosca, Jr, P. "Spontaneous combustion in the marshes of southern Louisiana." *Ecology*, **12**, 439-42, 2 figs., 1931.
- Wallace, A. R. *A narrative of travels on the Amazon and Rio Negro*. London, ed. 1889.

#### APPENDIX

##### *Notes on the Berbice savannahs*

These extensive savannahs lying west of the Berbice River, and 60-90 miles inland, at an elevation of 80-90 ft. above sea-level, have been the subject of a very careful botanico-ecological survey by Mr Martyn, Government Botanist (1931). These notes are merely supplementary to his work and deal mainly with the more southern grasslands between Yawakuri, where the cattle trail emerges from the forest, and Waranama, which was the site of his survey.

Martyn remarks that the principal grasses flowering at the time of his visit were *Trachypogon plumosus*, *Axonopus aureus*, *Andropogon leucostachys* and

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*Aristida setifolia*, in order of abundance. "The first three named grasses, together with the sedge *Rhynchospora pterocarpa*, constitute the greater part of the vegetation." When we add that the dominant savannah trees and bushes are *Curatella americana*, *Byrsonima crassifolia* and *B. coccolobaefolia* it will be seen that, save for specific differences in *Andropogon* and *Rhynchospora*, the vegetation is essentially the same as that of the Rupununi savannahs. A striking difference is the apparent absence of *Paepalanthus*.

The landscape is similar, but the rolling country is diversified by more frequent and larger bush islands and wider zones of fringing forest than in the Rupununi. At a similar season, probably in response to a higher rainfall, the Berbice savannahs appear much greener and the growth of grass more luxuriant, usually waist-high. A very striking feature, which I find it difficult to explain, is the nightly occurrence of heavy dews, drenching the grass tufts. Such dews are unknown in open savannah of the Rupununi, where the soil is generally sandy. I saw none of the perdigon or pebbly areas so frequent in the more southern savannahs.

Martyn estimated that at Waranama, *Trachypogon plumosus* formed about one-quarter of the grass-sedge association. Further south I am sure its contribution is very much more. The grass *Leptocoryphium lanatum* occurs not only near forest, as Martyn found, but also occupies considerable areas of flats between the undulations of the savannah. In these areas, when in flower, it appeared completely to dominate the *Trachypogon*, though the tufts of the latter were actually the more abundant. Other similar flats are occupied by *Sporobolus cubensis*, also in association with *Trachypogon*, and sometimes with *Leptocoryphium*.

In one respect the Berbice savannahs resemble the upland meadows of the Pakaraimas more than the lower grasslands of the Rupununi, and that is in the abundance of *Palicourea rigida*, over large areas taking the place of *Byrsonima verbascifolia*, which it so closely resembles in habit.

It is a curious fact that the leached white sand or muri areas, with an extremely specialised vegetation excellently described by Martyn, are here interspersed in the savannah country, whereas further south—between the Essequibo and the Berbice and in the Pakaraimas—they occur, with the same plant covering, as islands in otherwise continuous forest, and are hardly met with in savannah.

# THE EFFECT OF CONSTANT AND FLUCTUATING TEMPERATURE ON THE GERMINATION OF THE WEED SEEDS IN ARABLE SOIL

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(*With seven Figures in the Text*)

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## I. INTRODUCTION

IN the course of the work carried out on the weed flora of the Broadbalk wheat field at Rothamsted (Brenchley and Warington, 1930 and 1933), certain points of interest arose which seemed to merit further investigation. Criticism could naturally be levelled against the preliminary washing process to which the soil was subjected before the germination tests were started, as it was conceivable that such treatment might hasten or retard the emergence of the buried seeds from dormancy. Further, it was unknown to what cause the marked periodicity in germination evinced by certain species was due, whether to some external factor such as changes in temperature, or to something inherent in the seeds themselves. The present work was undertaken with a view to gaining some information on these points.

## II. PRELIMINARY EXPERIMENT

A. *Experimental procedure*

For the purpose of this experiment the same three plots on Broadbalk field were chosen as were being used for the main weed seed investigation then in progress. In January 1932<sup>1</sup> two bulked samples, each consisting of four borings, were taken on each of the three plots, one from a fallow and one from a cropped section in each case, the total area represented per bulked sample being  $\frac{1}{3}$  sq. ft. to a depth of 6 in. After well mixing, every sample was weighed, and two portions of  $1\frac{1}{2}$  lb. each put directly into germinating pans. The remaining and largest portion was then washed with a hose on a sieve until its size was sufficiently reduced for it to go into a pan of the same dimensions as the unwashed portions, i.e. diameter 20 cm. Experience had shown that a sieve, 50 linear mesh to the inch, could safely be used for this washing process without any loss of seed being incurred. The apparatus and method employed have been fully described in a previous publication (Brenchley and Warington, 1930). As the original samples varied in weight the factor necessary to compare the numbers of weeds from the washed and the unwashed portions varied according to the sample. An illustration of this is given as follows:

		Plot 7 lb.	Plot 18 lb.
Total weight of soil	... ..	15.75	14.5
Weight of soil untreated (a)	... ..	1.5	1.5
Weight of soil untreated (b)	... ..	1.5	1.5
Weight of soil washed	... ..	12.75	11.5
Factor: washed/untreated	... ..	8.5	7.7

Similar factors for the other four samples were 6.1, 7.7, 7.5 and 7.7 respectively. Though it was realised that the use of such a factor might be a source of error owing to the magnification of small values, yet the differences between the various treatments were so marked that the conclusions drawn from them are unlikely to have been affected.

Information was also desired as to the effect of changes in temperature on germination. All the samples, therefore, were placed at once in a cellar where the daily variations in temperature were almost negligible, the fluctuations that did occur taking place only gradually. The main weed seed experiment, which was in progress in the glasshouse at the same time, provided material for comparison, for in this case the daily temperature changes varied widely. A fuller discussion of the precise conditions, in each case with relevant data obtained from the self-recording instruments, is given in a later section (Fig. 1).

The seedlings that germinated were identified, counted and removed at frequent intervals, the soil being thoroughly stirred up every 6 weeks to ensure

<sup>1</sup> The setting up of this preliminary experiment was undertaken by Miss J. Martyn, B.Sc., who was also responsible for the oversight of the pans during the first seven months of the experiment.

that all seeds in turn came into a favourable position for germination. Little difficulty was experienced in identifying the seedlings in spite of their etiolated condition, for only a limited number of species germinated and most of these had well-defined characteristics. In several instances the testa remained attached to the cotyledons after their emergence, and by comparing this with actual seeds of which the identity was certain, confirmation or otherwise of the identification could be made. Supplies of water were kept standing in the cellar and later also in the incubator, in order to avoid introducing changes of temperature when watering.

### B. *Effect of washing soil on germination*

It was soon evident that the actual process of washing the soil had little or no effect on the number of species of seeds that germinated (Table I). In both cases the numbers from the fallowed sections are somewhat higher than from the cropped portions and the mean values are of much the same order. The smaller quantity of seedlings from the cropped sections was to be expected, as this part of the field had been recently fallowed for 2 years, so that the numbers of weeds had been considerably reduced in the preceding seasons.

Table I. *Comparison between germination from equal weights of washed and unwashed soil kept in cellar. All species together*

January–July 1932		Mean
Washed: Fallow section	111	84
Cropped section	56	
<sup>1</sup> Unwashed: Fallow section	90	78
Cropped section	66	

<sup>1</sup> Factor used to allow for smaller weight of soil.

### C. *Effect of external conditions on germination*

The outstanding result of the experiment was the exceptionally small number of seeds that germinated in the cellar compared with the high figures that experience had shown were normally to be expected with similar soil under glasshouse conditions. Strictly comparable data from samples started simultaneously in the glasshouse are not available for this experiment, but subsequent investigations establish the inferiority of germination under cellar conditions.

The number of species comprising the weed flora from these pans in the cellar was also very much reduced. It did not seem likely that these differences could be attributed wholly to the fact that the soil samples were taken in January whereas the earlier experiments had been started in the autumn. The obvious conclusion was to regard the result as mainly due to differences in temperature, since it appeared unlikely that changes in humidity or light would have such a marked influence on germination of seeds in soil. Further investigations in this direction were accordingly made, and eight of the pans

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(two from the washed and six from the unwashed series) were transferred to the glasshouse after 6 months, the remainder being left behind as controls. An immediate response to the changed conditions was obtained, a quantity of seedlings of various species appearing in all pans soon after the transfer was made, whereas no change in the behaviour of the pans left in the cellar occurred. After a further 12 months, three more pans were removed to the glasshouse with similar results, and finally, after 2 years, all the remaining pans were taken out of the cellar. A more detailed study of the figures showed that all species were not behaving similarly, *Alopecurus agrestis* in particular reacting in quite a different manner from the other species. Although the numbers were never large, *Alopecurus* germinated more freely in the cellar than any other weed except *Alchemilla arvensis*. Removal to the glasshouse, however, brought about an increase in germination in all species except *Alopecurus*, as Table II shows. No comparison is available in this series for pans kept all the time in the glasshouse for a similar period, but data on this point are given in a later section (p. 197, Table V).

Table II. *Number of seeds germinating per pan in 3 years. Average of three pans after calculating to same weight of soil*

	Cellar (first 18 months)	Glasshouse (second 18 months)
<i>Alopecurus</i>	91	13
Other species	47	520

### III. MAIN EXPERIMENT

#### A. *Experimental procedure*

This evidence of specialised behaviour on the part of certain species seemed to warrant more detailed investigation, and in August 1932 and 1933 further soil samples were taken simultaneously with, and from the same three plots as, those intended for the principal weed seed investigation in progress at the time. Three borings were made for each bulked sample, the total area represented per pan thus being  $\frac{1}{4}$  sq. ft. to a depth of 6 in.

The plots selected received farmyard manure (plot 2), complete minerals with nitrogen (plot 7) and minerals or nitrogen in alternate years (plot 18) respectively, so that weeds of all types were represented. The field at the time was being fallowed in sections, but these additional samples were taken from parts that had been back under crop for 2 or 3 years since their turn of fallow, and were likely to contain a fair number of weed seeds.

All the samples were subjected to the washing treatment to reduce their bulk to a convenient size, after which half of the 1932 pans (two from each plot) were taken at once to the cellar, their duplicates being placed in an electrically controlled incubator, while all of the 1933 pans were put into the cellar. The samples prepared at the same time for the main weed seed experiment in both 1932 and 1933 were taken direct to the glasshouse as usual. The incubator was fitted with a glass door, so that light was not altogether excluded.

Comparison was thus available between soil identically treated, but from which germination could be studied under the following conditions:

- (1) Small daily fluctuations in temperature and almost complete darkness (cellar).
- (2) Small daily fluctuations in temperature and subdued light (incubator).
- (3) Large daily fluctuations in temperature and bright daylight (glass-house).

The pans were kept in their respective places<sup>1</sup> for 1 year. After this period had elapsed one-half of the 1932 series in the incubator and cellar respectively were transferred to the glasshouse, three pans being left behind as controls in each case. After a further 12 months two of each of the latter were taken to the glasshouse, this time only single pans being available as controls: these, however, proved sufficient, as their behaviour exactly confirmed the other results. Similar transfers were made with the 1933 series, but as the data, though entirely consistent (cf. Figs. 2 and 4), are not yet complete,<sup>2</sup> the discussion that follows will be based chiefly on the earlier (August 1932) experiment.

As has already been stated, the soil samples were taken from three differently manured plots on the wheat field. The abundance of weeds varied considerably in the three cases, plot 7 generally yielding much heavier crops of seedlings, particularly *Alchemilla arvensis*, than either plot 2 or plot 18. Where possible the data given are based on the averages of the three plots, but when pans were transferred from one set of conditions to another it was impossible to get representatives from each plot for each treatment. The set containing the samples from plot 7 tended, therefore, to give germination figures decidedly higher than the others, but as all the results lay in the same direction any differences introduced in this way can be disregarded. It does, however, explain one or two apparent discrepancies in the figures which might otherwise be attributed to error in calculation.

At this point, some account of the temperature conditions that prevailed in the cellar, incubator and glasshouse respectively is necessary before the results can be discussed.

#### B. *Temperature conditions in cellar, incubator and glasshouse*

Self-recording instruments were placed with each of the three sets of pans, and Fig. 1 shows the weekly averages of the daily maximum and minimum readings obtained throughout 1934. The graph for the preceding year was almost identical. A large scale has been used for the sake of clarity, as the maxima and minima curves for the cellar and incubator run so close to each other.

<sup>1</sup> Temporary removal to another cellar and incubator was unavoidable for a few weeks, but the transfer was made with every precaution, and the temperatures recorded in the new situations showed little or no change from those originally intended.

<sup>2</sup> Since this paper went to press, further data for the 1933 series have become available, and transference to the glasshouse after 2 previous years at constant temperature again caused a sudden and marked rise in germination, thus entirely confirming the results in Fig. 3.



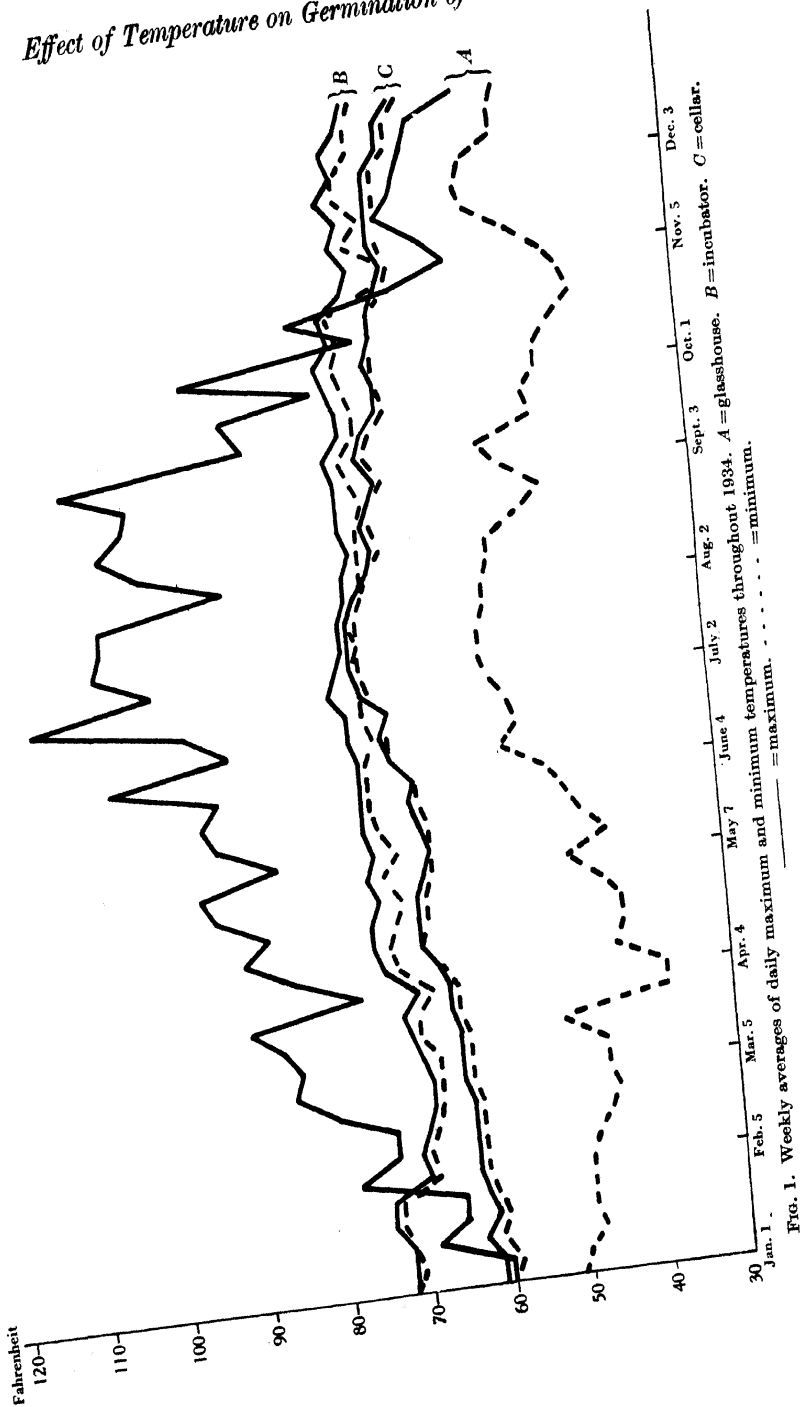


FIG. 1. Weekly averages of daily maximum and minimum temperatures throughout 1934. A = glasshouse. B = incubator. C = cellar.

(i) *Cellar*. Although not thermostatically controlled the temperature kept remarkably constant, the average weekly difference between the daily maxima and minima never reaching 1° F. in 3 years. Although the entire range over which the weekly averages varied was as much as 55–70° F., 52–74° F., and 59–74° F. in 1932, 1933 and 1934 respectively, the rise or fall was so gradual that its effect was probably almost negligible.

(ii) *Incubator*. Trouble was experienced in maintaining a completely constant temperature with the apparatus available and the daily fluctuations actually exceeded those in the cellar, the average weekly difference between the maxima and the minima recorded being 1.6 and 1.8° F. in 1933 and 1934 respectively. On the other hand, the total extent of the temperature variation during the year was slightly less than in the cellar, the average weekly maxima and minima ranging from 60 to 76° F. and 66 to 77° F. in 1933 and 1934 respectively. Compared with the glasshouse, however, the fluctuations were almost negligible, and it was thought wiser to carry on with the apparatus, even if the conditions were not ideal, rather than vitiate the continuity of the experiment by transferring the pans elsewhere. The results showed that this procedure was entirely justified.

(iii) *Glasshouse*. In this case the variations in temperature were very marked indeed, particularly during the summer months, when as great a difference as 60° F. in 1 day sometimes occurred. Artificial heating of the house in winter resulted in more level temperatures, but even then the daily variations were of the order of 10–20° F., i.e. very considerably greater than those that obtained in the incubator or cellar. From the literature it is clear that alternations in temperature may exert a marked effect on germination of some seeds, and also that the type of alternation may be important. Morinaga (1926), for example, found that *Cynodon dactylon* L. (Pers.) definitely required an alternating temperature for germination, but that provided the exposure to either the high or low temperature was for at least 4½–8 hours it was immaterial at which level the longer period was spent. Doerfel (1930), on the other hand, showed that certain species, *Hyoscyamus* for example, germinated best when exposed for a shorter time at the lower than at the higher temperatures, and that the difference between the two levels needed to be sufficiently large before any improvement was obtained, an alternation as small as from 25 to 30° C. actually proving harmful. The behaviour of *Lysimachia*, however, was in the opposite direction, for this species required the longer time at the lower temperature. Similarly, Harrington (1923), found that the exposure of parsnip and celery seed to alternations of 20° C. for 16½ hours and 30° C. for 7½ hours improved germination, but if the times in the two chambers were reversed, no improvement was obtained. Further, he showed that with several species the exposure to the higher temperatures was only desirable if the time did not exceed 6–8 hours and that the change over to the lower temperature should be fairly rapid. The thermograph records obtained

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from the glasshouse during 1934 were therefore inspected in detail with a view to seeing how the conditions there compared with those with which Harrington worked. A number of days were selected of widely differing types and the length of time determined during which the temperature was above the mean for the day. Although this period was frequently as much as 8 hours, it was very rarely greater, and it is interesting to notice that on two days quite extreme in type (the difference between the maxima and minima being 61 and 12° F. respectively), the length of time for which the temperature was above the mean for the day was 6 hours in each case. An important point of difference between the conditions used by Harrington and those in the present work was that in the former case sudden alternations of temperature between fixed maxima and minima were employed, whereas in the Rothamsted glasshouse experiment the change of temperature was more gradual and fluctuated between maxima and minima that varied from day to day. Considering these marked differences in technique the similarity in results is particularly striking.

### C. *Effect of light on germination*

In view of earlier work, the possibility of differences in illumination exerting an influence on germination cannot be overlooked. Gassner (1915), for example, showed that certain types of seeds such as *Oenothera* and *Epilobium* germinated better in the light than in the dark, whereas the reverse was the case with *Clarkia* or *Phacelia*. Pickholz (1911), however, showed that in the case of *Poa pratensis* the improvement in germination brought about by exposure to light was in reality due to the temporary changes in temperature incidentally incurred and not to any direct action of the light as such. In order to ensure that any differences obtained in germination in the cellar or incubator compared with the glasshouse were not really due to differences in light conditions, four additional pans of soil from the same field were set up in the glasshouse in February 1935. Two of these were allowed full daylight, while the other two were placed inside a large box covered with a dark cloth and lid. The variation in temperature inside the box was inevitably rather smaller than in the glasshouse itself, especially as many days of bright sunshine occurred during the course of the experiment, but as the average difference between the daily maximum and minimum readings over a 40-day period amounted to 17 and 39·6° F. for the box and glasshouse respectively, all four pans may be regarded as having been exposed to definite fluctuations in temperature. Seeds of *Papaver rhoeas*, *Alopecurus agrestis*, *Capsella bursa pastoris*, *Stellaria media*, *Plantago major* and *Veronica buxbaumii* were sown in every pan and the experiment was carried on for 40 days, after which time germination practically ceased. *Alopecurus*, *Papaver*, *Plantago* and *Veronica* all germinated rapidly and freely under both sets of conditions, providing definite proof that the almost complete absence of *Papaver* seedlings in pans kept in

the cellar and incubator was due to a lack of sufficient fluctuation in temperature and not to any deficiency in light. The same conclusion applies to *Stellaria media*: this species came up much more freely in the pans inside the box than outside in the glasshouse, but under conditions of constant temperature it fails to appear even in the absence of light. *Capsella bursa pastoris*, on the other hand, behaved in an exceptional manner, showing a marked preference for germination in the light. In this case, therefore, the lack of light in cellar or incubator may have been the reason why this species failed to germinate until the soil samples were transferred to the glasshouse.

It seems, therefore, safe to assume that in the majority of cases the failure of the weed seedlings to appear while in the cellar and incubator was directly due to insufficient fluctuations in temperature and not to any lack of light. The fact that the results from samples kept in the incubator where a certain amount of light was allowed to penetrate were in general similar to those in the cellar confirms this conclusion.

#### D. Germination of weeds in cellar, incubator and glasshouse

It has already been indicated that conditions in the cellar seriously inhibited germination, and it was soon evident that the same result was being obtained in the incubator. All species, however, were not equally affected (Table III). *Alopecurus agrestis* and *Alchemilla arvensis* were the only weeds that germinated at all freely under the approximately constant temperatures, but their numbers were still decidedly below those obtained in the glasshouse. A few specimens of *Papaver rhoeas*, *Veronica hederifolia*, *V. arvensis*, *Medicago lupulina*, *Scandix pecten* appeared, while *Stellaria media*, *Caucalis arvensis*, *Myosotis arvensis*, *Galium aparine* and one or two unidentified seedlings were of even rarer occurrence.

Table III. Total germination per pan ( $\frac{1}{4}$  sq. ft.) in first year  
August 1932-3. Average of all three plots

	<i>Alopecurus</i>	<i>Alchemilla</i>	<i>Papaver</i>	All species
Glasshouse	142	145	217	606
Cellar	45	20	6	80
Incubator	71	59	9	56

The question naturally arose as to the fate of the seeds, presumably present in the soil, which failed to germinate. Two possibilities suggested themselves, *viz.* that the unfavourable conditions had either induced a temporary dormancy which would disappear when the inhibiting influences were removed, or that the seeds had failed to survive the stay in the incubator or cellar, in which case no germination would ensue even if the conditions again became favourable:

E. *Effect of transferring soil samples from cellar and incubator to glasshouse*

The result of transferring pans from the cellar or incubator to the glasshouse is best illustrated in the form of graphs, and Figs. 2, 3 and 4 show the total numbers of seedlings obtained per pan plotted at 6-weekly intervals during the various phases of the experiment. *Alopecurus* has been omitted here, as its behaviour was in complete contrast to all other weeds, but a full account of it is given in a later section (p. 198, Fig. 5).

During the first years in the cellar or incubator the germination curves showed slight and probably indefinite fluctuations, but though the occurrence of a peak period between January and March is suggested the figures are too small for any definite claim for seasonal behaviour to be made. Removal to the glasshouse at the end of the first or second year brought about an immediate response, a number of seedlings of a variety of species germinating at once, just as had been found in the preliminary experiment. This is shown by an immediate sharp rise in the curve, the highest level being obtained in October, after which a rapid fall ensued. The minimum was reached in July, to be followed by a further peak in the next October. The smaller size of the second maximum was of course due to the large numbers of seeds that had already been worked out of the soil.

In order to interpret these results satisfactorily, comparison must be made with the germination in pans kept in the glasshouse throughout. Here a distinct seasonal periodicity was shown, as has been consistently found in experiments of this nature, a maximum germination of the majority of the species occurring each winter between October and January, and a minimum about July. Although the transfer of samples from the cellar to the glasshouse in August caused an immediate increase in germination, it will be noticed that the maximum did not occur until October, and that the peak in the following year also appeared in the same month, i.e. the samples at once fell into line with those kept in the glasshouse throughout. Earlier experience with soil germination tests started in the early part of the year have shown that hardly any *Alchemilla* seedlings will appear until the following autumn and winter, as they have a definite preference for germination at this season. As this species was one of the most plentiful in the soil used for the present experiment, its behaviour probably accounts for the slight delay in the attainment of the maximum point even when the conditions unfavourable for germination had been removed. A striking confirmation of this is given by the pans set up in the preliminary experiment in January 1932, for here the transfer from the cellar took place in July, a time of year when germination is at a minimum. As already stated a rush of seedlings occurred, but even these were relatively few in number, the majority waiting until October before germinating (Table IV).

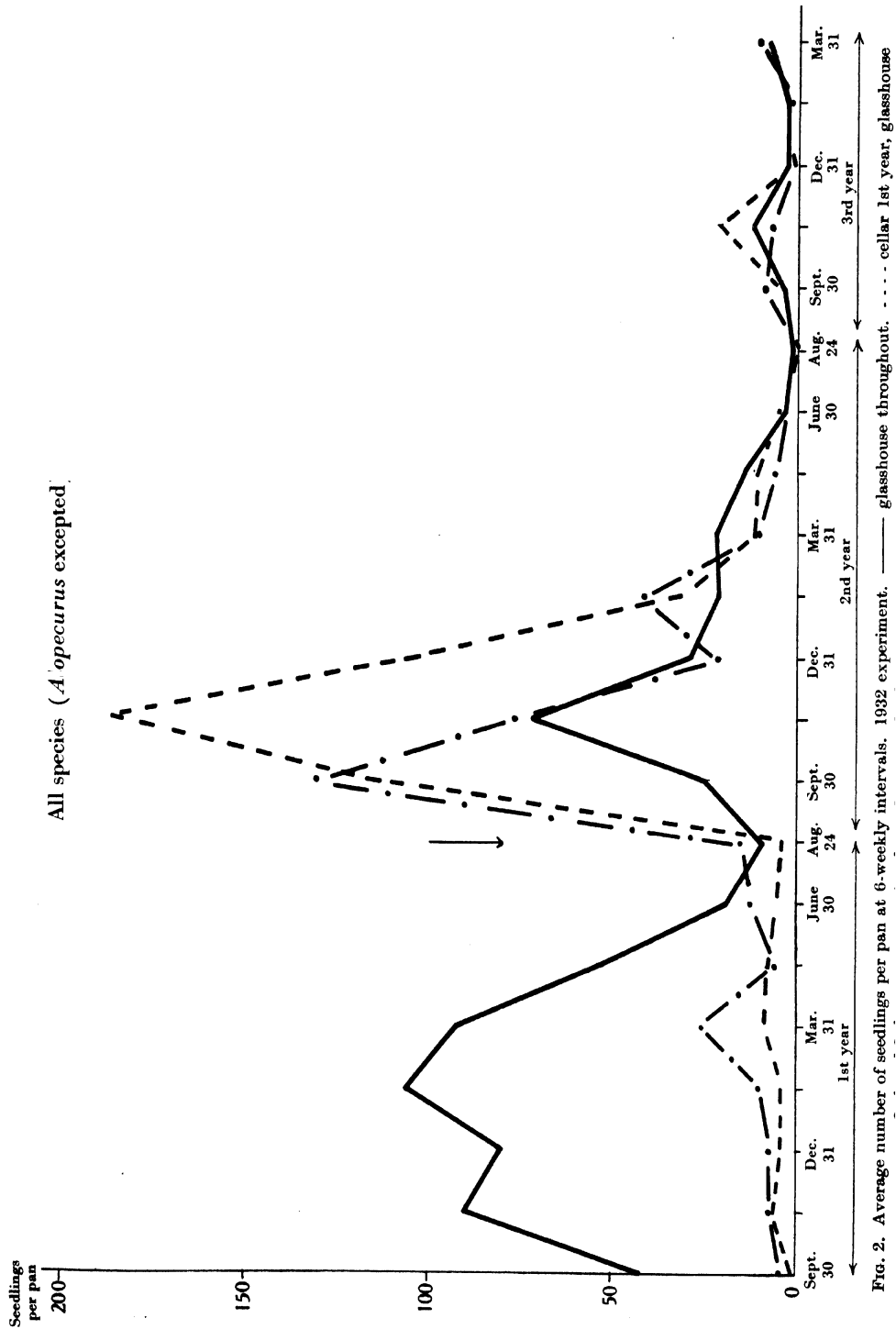


Fig. 2. Average number of seedlings per pan at 6-week intervals. 1932 experiment. — glasshouse throughout. - - - cellar 1st year, glasshouse

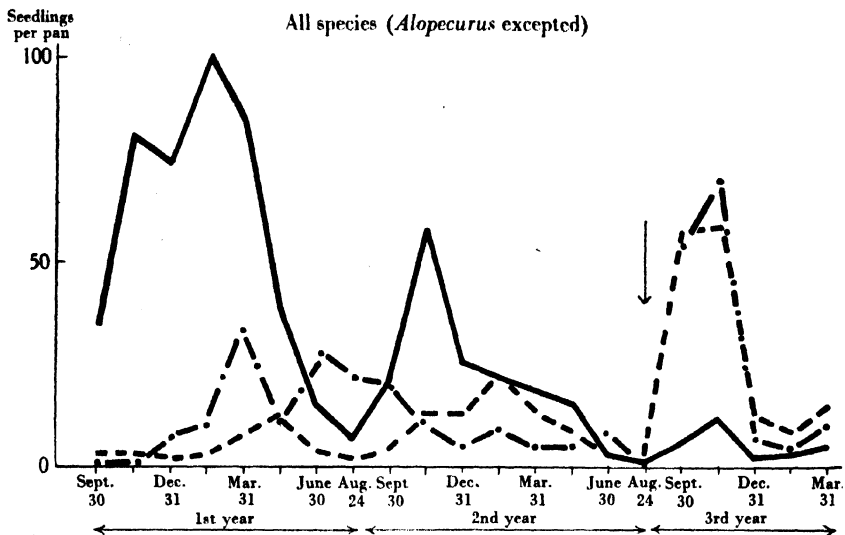


FIG. 3. Average number of seedlings per pan at 6-weekly intervals. 1932 experiment. — glasshouse throughout. - - - cellar 1st and 2nd years, glasshouse 3rd year. - · - incubator 1st and 2nd years, glasshouse 3rd year. Arrow denotes date of transfer.

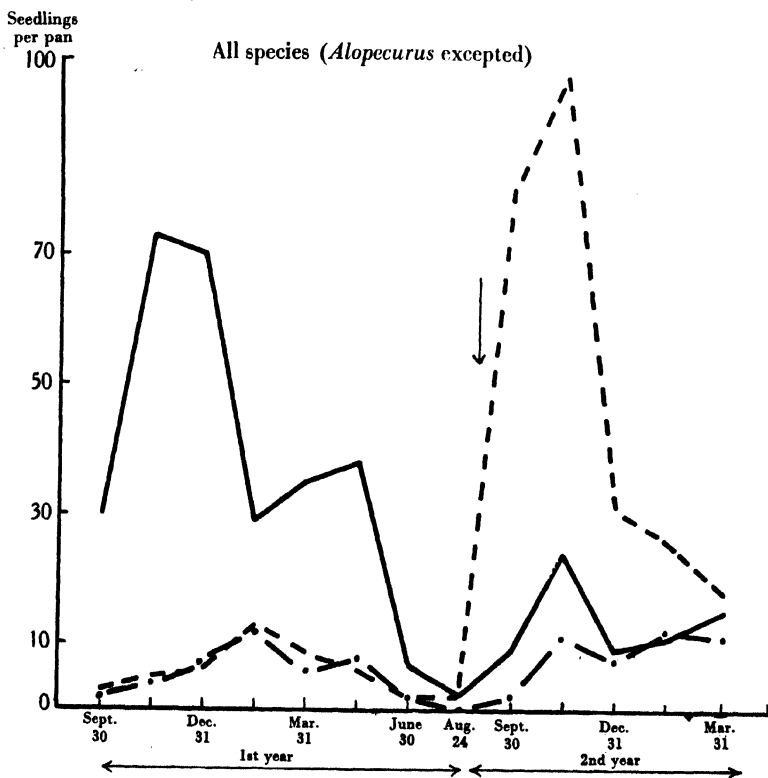


FIG. 4. Average number of seedlings per pan at 6-weekly intervals. 1933 experiment. — glasshouse throughout. - · - cellar throughout. - - - cellar 1st year, glasshouse 2nd year. Arrow denotes date of transfer.

Table IV. *Effect on germination when soil samples were transferred from cellar to glasshouse in July*

	Total for 6 months in cellar, Jan. 19-July 19	Approx. 6 weekly records, July 20-Dec. 31				Total
<i>Papaver</i>	17	—	—	—	—	—
<i>Alchemilla</i>	7	—	1	7	1	9
*Other species	6	—	—	—	—	—
<i>Papaver</i>	10	14	8	44	17	83
<i>Alchemilla</i>	2	4	5	72	22	103
*Other species	24	6	11	17	3	37

\* *Alopecurus* excluded.

The behaviour of the pans left behind for a second year in the cellar or incubator as controls is illustrated by Fig. 3, where it is clear that the curves followed precisely the same course as in the first year. Removal to the glasshouse even after this prolonged period, however, brought about a sudden increase in germination, though the numbers of seedlings were definitely lower than when the treatment had been continued for 1 year only, presumably owing to the failure of a certain number of the seeds to survive the unfavourable conditions for so long a time. Even after a single year's treatment in the cellar or incubator fewer seedlings were obtained than would be normally expected had all seeds shown the requisite capacity for continued dormancy. These results are also confirmed by the figures given in Table V, where the total numbers of seedlings of all species obtained under the varying combinations of cellar, incubator and glasshouse conditions during the whole course of the experiment (2½ years) are given.

Table V. *Mean germination per pan over a 2½-year period under varying conditions*

Conditions	Years	<i>Alopecurus</i>	<i>Alchemilla</i>	<i>Papaver</i>	All species together
Glasshouse	2½	156	248	303	865
Cellar	2½*	18	28	8	67
Cellar	2	26	88	11	147
Glasshouse	½	1	42	104	152
Cellar	1	69	22	7	111
Glasshouse	1½	8	222	228	513
Incubator	2½*	20	21	7	69
Incubator	2 †	32	138	11	204
Glasshouse	½	—	41	92	144
Incubator	1	114	53	10	200
Glasshouse	1½	21	66	163	336

\* Plot 7 not included.

† Germination from plot 7 sample abnormally high in incubator.

Closer inspection was, however, desirable to see if all species were being similarly affected by the treatments or whether some were more able to survive a period of unfavourable conditions than others, as the preliminary work had suggested.



F. *Response of individual species to conditions in cellar, incubator and glasshouse*

(i) *Alopecurus*. In the preliminary experiments (Table II, p. 188) indications had been obtained that of all the weed seeds encountered in the Broadbalk soil, the germination of *Alopecurus* was the least adversely affected

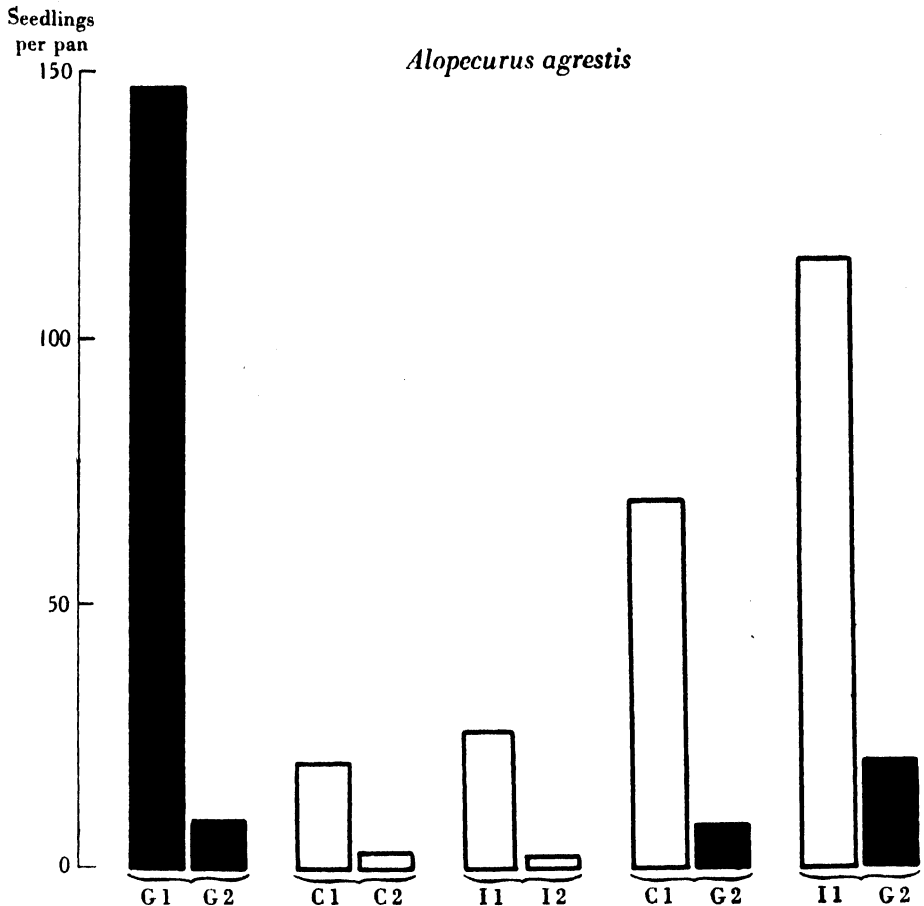


FIG. 5. Average number of seedlings of *Alopecurus agrestis* per pan per year. G=glasshouse (black). C=cellar (white). I=incubator (white). 1 and 2 denote 1st and 2nd year of experiment.

by conditions in the cellar. Confirmation of this point was, however, desirable, because the early figures had involved the use of a factor to compensate for differences in size of soil sample, and were in consequence open to criticism. Both of the main experiments with samples taken in August 1932 and 1933 entirely bore out the earlier results, and Fig. 5 illustrates the course of events for the 1932 series. It is quite clear that the conditions in the cellar and

incubator did not by any means prevent the germination of *Alopecurus* seeds, although the numbers of the seedlings appearing in these samples were generally considerably smaller than from the corresponding pans in the glass-house. Also practically all the seeds that germinated did so during the first year, irrespective of the conditions under which the samples were kept. Further, transfer of pans to the glasshouse after a prolonged stay in the cellar

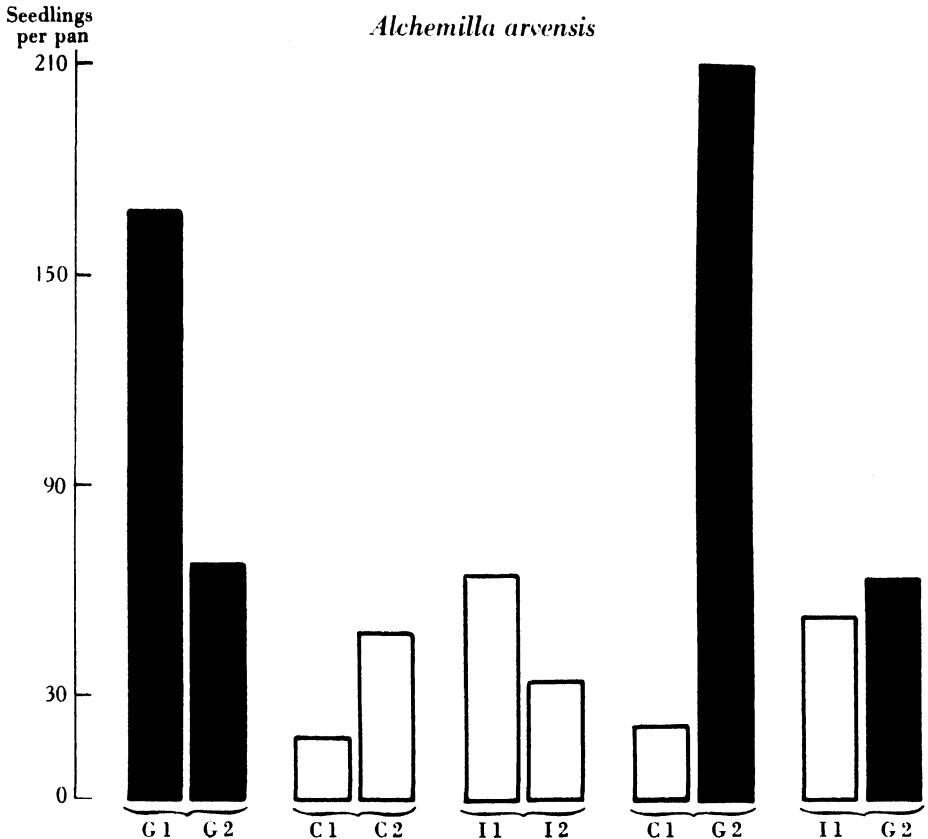


FIG. 6. Average number of seedlings of *Alchemilla arvensis* per pan per year. G = glasshouse (black C = cellar (white). I = incubator (white). 1 and 2 denote 1st and 2nd year of experiment.

or incubator did *not* result in any increase in the germination of *Alopecurus*. Considerable loss by death must, therefore, have occurred while the samples were in the cellar and incubator, for if the seed had merely been in a dormant condition it would have survived the temporarily unfavourable circumstances. The short natural life of this species suggested that it might be a principal cause of the loss of seedlings incurred by a prolonged stay in the cellar to which reference has already been made (Table V), and further investigation into the behaviour of the other principal weeds showed this to be the case.

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(ii) *Alchemilla arvensis* was the only other species besides *Alopecurus* that germinated in any quantity under cellar or incubator conditions, but the numbers never reached anything approaching those obtained from samples in the glasshouse (Fig. 6). In other respects, however, the behaviour of *Alchemilla* was in striking contrast to that of *Alopecurus*. By no means all the seeds germinated during the first year, either from the samples in the glasshouse, cellar or incubator, and further, transfer to the glasshouse of pans kept for the first 12 months in the cellar resulted in a rapid and prolific germination of this species. *Alchemilla* evidently possesses a considerable capacity for survival, since 1 year's exposure to cellar conditions made practically no difference to the total number of seedlings obtained during the whole course of the experiment. The figures for the incubator samples were less satisfactory, since only one of the three replicates (viz. the sample from plot 7) showed this response. Whether this inconsistency was due to the fact that the samples not falling into line contained an unusually small initial stock of *Alchemilla* seed or not is uncertain, but complete confirmation of the results from the cellar pans was obtained in the succeeding year when transfer to the glasshouse again caused a marked increase in germination (Table VI).

Table VI. *Germination of Alchemilla under cellar and glasshouse conditions.*  
*Average per pan. 1933 experiment*

	First Year				Second Year	
	Aug.-Nov.	Dec.-Feb.	Mar.-May	June-Aug.	Aug.-Nov.	Dec.-Feb.
Glasshouse throughout	38	35	29	2	13	10
Cellar throughout	4	12	11	2	11	15
Cellar, 1st year; glasshouse, 2nd year	3	12	11	2	65	27

(iii) *Papaver rhoeas*. This is the most prolific of all weeds in the Broadbalk soil, so that well-defined results were to be hoped for with this species. Its behaviour proved to be a complete contrast to that of *Alopecurus*, a considerable proportion of the seedlings germinating in the second year of the experiment as earlier experience had already shown was characteristic of this weed under glasshouse conditions (Brenchley and Warrington, 1933). Further, hardly any *Papaver* seedlings appeared in the samples so long as they were kept in the cellar or incubator, but transfer to the glasshouse brought about an immediate response (Fig. 7). This could not have been induced by the action of light, since, as has been already shown, *Papaver* germinates readily in pans kept in the dark but exposed to a fluctuating temperature. *Papaver* apparently possesses a fairly strong natural capacity for survival during unfavourable conditions, and large numbers were able to germinate when suitable circumstances were forthcoming. Their viability, however, seems to be somewhat less than that of *Alchemilla* (Table V).

(iv) *Other species*. Only a few isolated individuals of species other than those mentioned above appeared in the pans while they were kept in the cellar

or incubator, but on removal to the glasshouse the normal heterogeneous flora consisting of such species as *Myosotis arvensis*, *Matricaria inodora*, *Veronica hederæfolia*, *V. arvensis*, *Arenaria serpyllifolia*, *Stellaria media*, *Legousia hybrida* and *Bartsia odontites* immediately developed. The actual numbers of these seedlings per pan were small, but when considered together they are sufficiently convincing to show that in general their non-appearance was due to unfavourable conditions of temperature. *Veronica hederæfolia* and *V. arvensis* may be quoted as typical of these less plentiful weeds (Table VII).

Seedlings  
per pan

*Papaver rhoeas*

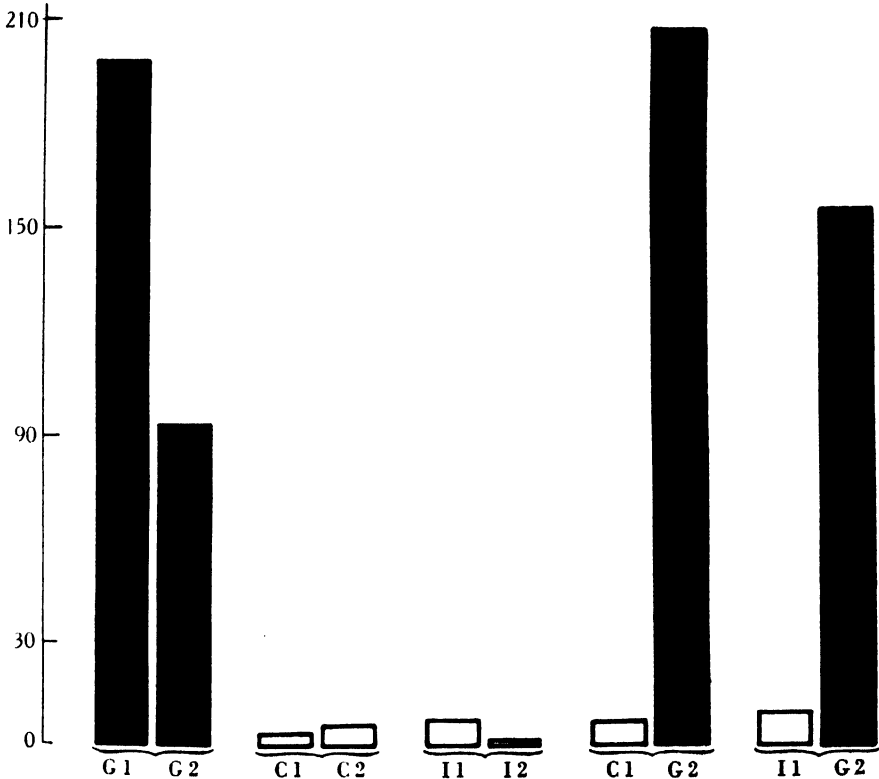


FIG. 7. Average number of seedlings of *Papaver rhoeas* per pan per year. G=glasshouse (black). C=cellar (white). I=incubator (white). 1 and 2 denote 1st and 2nd year of experiment.

Table VII. Germination of *Veronica hederæfolia* and *V. arvensis* under cellar and glasshouse conditions. Average per pan. 1933 experiment

	First year, Aug. 1933–Aug. 1934	Second year, Aug. 1934–Mar. 1935
Glasshouse throughout	40	2
Cellar throughout	7	6
Cellar, 1st year, glass- house, 2nd year	7	25

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The fact that *Veronica hederæfolia* responded to the change over to glasshouse conditions is all the more remarkable, since Ebner (1924) definitely describes it as a "Dunkelkeimer". Fluctuations in temperature were, therefore, of even greater importance to germination than the light factor, for although the soil covering would naturally prevent any harmful action of direct light, seeds near the surface were frequently noticed to be germinating in pans exposed to the bright light of the glasshouse. One other interesting point was noticed with this weed when the pans were transferred to the glasshouse in August. The seedlings showed a definite tendency to make their first appearance in September, whereas previous experience had shown, in correspondence with Ebner's findings (1924), that this species normally only begins to germinate in October. The effect was particularly striking to the eye as the transferred samples were placed side by side with the pans kept under glasshouse conditions all the time.

One other weed calls for special mention, viz. *Medicago lupulina*. This species is very sporadic in appearance in the field, being prolific in some years but comparatively rare in others. It is somewhat late in developing and when plentiful is a striking feature on the stubble. In certain seasons (the impression from observations being that moist conditions are favourable) numerous *Medicago* seedlings begin to develop at once before the land is ploughed up. The year 1932 was noteworthy for the abundance of *Medicago* on Broadbalk field, and in consequence the samples taken in August of that year contained large quantities of seed. These were so impatient of delay that they came up in glasshouse, cellar and incubator alike within 1 or 2 days after the soil had been washed and set up into pans, the washing process possibly having some encouraging effect on germination. As many as 148 *Medicago* seedlings appeared in a single pan in the cellar within a short time, but since it was obvious that these seeds had not come under the influence of the different temperature conditions as the experiment intended, all figures for *Medicago* were discarded for the first 6 weeks. Later germinations of this species, however, were taken into account in the usual manner.

### IV. DISCUSSION

It was stated at the outset of this paper that these experiments had been carried out with a view to seeing firstly, if subjecting soil samples to a washing process to reduce bulk affected the germination of the weed seeds present, and secondly, if the seasonal periodicity in germination evinced by certain species could be associated with any external conditions such as temperature, or was to be attributed to some factor inherent in the seed itself.

The answer to the first question was readily obtained in the negative: the results from the second enquiry, however, seem to need some further discussion. A study of the temperature conditions prevailing in the cellar, incubator and glasshouse respectively, during the course of the experiment,

showed that whereas in the two former approximately constant temperatures were maintained, in the latter very marked fluctuations occurred. Since the majority of the weed seeds failed to germinate, or did so only sparingly when kept in the cellar or incubator, but responded immediately if transferred to the glasshouse, it may be inferred that many of the commonly occurring weed seeds are of the type for which alternations in temperature are required for good germination. Corroboration of this conclusion is provided by the observation that when soil samples are kept in an incubator at 30° C. for 3 weeks prior to chemical determinations, seedlings rarely develop. The fact that some seeds came up when the soil was kept at approximately constant temperature does not invalidate this conclusion, for it must be borne in mind that the stock present in a soil at any moment is composed of seeds of very different age and in all stages of maturity. Some of the seeds may already have been exposed to the requisite alternations in temperature and would, therefore, be ready to germinate at once even when those fluctuations ceased.

The tendency shown by certain weeds to germinate at special times of the year (periodicity) is probably linked up with various internal and external conditions of which the temperature at any stage in the life history of the seed presumably plays an important part. In support of this, germination of weed seeds that normally showed one peak period in the year when the soil samples were kept in a cold house during the winter, showed two maxima when heat was supplied (Brenchley and Warington, 1930). External factors alone, however, cannot provide the full explanation for this phenomenon of periodicity, since a weed such as *Alchemilla* will germinate chiefly in the autumn in spite of the fact that very similar temperature fluctuations also occur in the spring. Neither can it be solely a matter of the seeds needing a definite period of after-ripening, or one would expect a continuous spell of germination with a gradual falling off in numbers after the rush in the autumn, whereas actually the decrease is fairly sharp and is followed by a second maximum in the following autumn without any fresh seed having been introduced. It was unfortunate that no seedlings of *Polygonum aviculare* appeared in the samples under discussion, for this is definitely an early spring germinating type and a detailed study of this species in conjunction with *Alchemilla* might throw some light on the problem.

For the present, therefore, all that can be said is that periodicity is evidently due to a combination of factors of which temperature probably plays an important part.

## V. SUMMARY

1. Comparison between the germination of weed seeds from field soil which was first washed on a fine sieve with that which was left untreated showed that the washing process had no material effect on the germination of the species present.

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2. Germination of all species was very definitely inhibited if the soil was kept in a cellar or incubator where the daily fluctuations in temperature were very slight and the light wholly or partially excluded.

3. Some weed seeds were more adversely affected by the conditions in the cellar and incubator than others, *Alopecurus agrestis* being the least and *Papaver rhoeas* the most sensitive of the more important species encountered.

4. The inhibiting effect of the conditions in the cellar and incubator is attributed to the lack of sufficient fluctuation in temperature, rather than to the reduction in light intensity, though with certain species this also may have played a part in the results.

5. Removal of the soil samples to the glasshouse after 1 or 2 years in the cellar or incubator where few or no seedlings had appeared resulted in a rapid germination of a variety of weed seeds, showing that their failure to appear sooner was due to unfavourable conditions in the previous circumstances.

6. Too long an exposure to the conditions in the cellar or incubator resulted in a loss of seeds by death, the capacity for survival varying with the different species. *Alopecurus agrestis*, for example, generally failed to survive 1 year, whereas *Alchemilla arvensis* and *Papaver rhoeas* showed a viability extending to at least 2 years.

7. The reason for the seasonal periodicity in germination evinced by several species is discussed, but no conclusions are reached except that temperature conditions are apparently of great but not of sole importance.

### REFERENCES

- Brenchley, W. E. and Warington, K. "The weed seed population of arable soil. I." This JOURN. **18**, 235-72, 1930.
- Brenchley, W. E. and Warington, K. "The weed seed population of arable soil. II." This JOURN. **21**, 103-127, 1933.
- Doerfel, F. "Über den Einfluss des Frostes und intermittierender Temperaturen auf die Keimung verschiedener Samen." Bot. Arch. **30**, 1-50, 1930.
- Ebner, H. "Keimungsphysiologie von *Draba verna*, *Thlaspi perfoliatum*, *Holosteum umbellatum* und *Veronica hedaerifolia*." Öster. Bot. Z. **73**, 23-41, 1924.
- Gassner, G. "Altes und Neues zur Frage des Zusammenwirkens von Licht und Temperatur bei der Keimung lichtempfindlicher Samen." Ber. dtsh. Bot. Ges. **33**, 203-17, 1915.
- Harrington, G. T. "Use of alternating temperatures in the germination of seeds." J. Agric. Res. **23**, 295-332, 1923.
- Morinaga, T. "Effect of alternating temperatures upon the germination of seeds." Amer. J. Bot. **13**, 141-158, 1926.
- Pickholz, L. "Ein Beitrag zur Frage über die Wirkung des Lichtes und der intermittierenden Temperatur auf die Keimung von Samen, sowie über die Rolle des Wassergehaltes der Samen bei dieser Wirkung." Z. Landw. Versuchst. Öst. **14**, 124-51, 1911.

# AN ENALID PLANT ASSOCIATION IN THE HUMBER ESTUARY

By GRAHAM PHILIP

(With four Figures and three Graphs in the Text)

## HISTORICAL RECORDS

THE scarcity of records of the "sea-grass" vegetation of the Humber estuary is rather remarkable, when the importance of these plants to shore life is considered, and this therefore acted as a stimulus to an ecological study. In the "Flora of the East Riding of Yorkshire" (Robinson, 1902), *Zostera marina* L. is only casually mentioned as "cast up within Spurn head 1888", and it remained for Petch (1903), in a zoological paper, to record "*Zostera* pools, Skeffling to Spurn" as a habitat of littoral animals. The flora is indebted to Petch for records of *Ruppia rostellata* (Koch.) worded as follows: "Uncommon, tidal pools Easington 1900, and Patrington Haven 1901." It was therefore interesting, after a lapse of about 30 years, to confirm these records in August 1932, and to make a more detailed examination of this unique type of vegetation.

## DESCRIPTION OF HABITAT

The situation of the plants, on the northern shore of the estuary of the river Humber, is on Kilnsea, Easington and Skeffling "clays" inside the protecting curve of Spurn head. The latter, as well as protecting the plants from being uprooted by wave action, has allowed the deposition of estuarine silt in between Sunk Island and its promontory. This organic silt, brought down by the rivers which contribute to the Humber estuary, fertilises the sand deposited by the incoming tide. The deposition of fine silt, which in suspension accounts for the exceptional turbidity of Humber water, is probably activated by the incoming salt water. The ionised sodium chloride neutralising the charge on the electrified silt particles causes deposition and consequent accumulation in places, such as this, undisturbed by strong water currents. The mud flats, or clays as they are designated on the map, whilst under the influence of tidal disturbance, do not interfere with the main channel of the river. General observation indicates that the mud flats have a structure at the surface of laterally alternating hard and soft beds, plasticity being influenced by the relative proportions of sand and silt present. The deposition mechanism of this lateral alternation is more difficult to explain than the analogous vertical accretion described by Good and Waugh (1934). The flats are inundated completely even by neap tides, and their drainage therefore affects the sea-grass vegetation. At low tide they are the only intertidal place on this shore where



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standing water is not drained rapidly off by more or less steeply sloping mud banks. The formation of shallow pools 3–6 in. deep, due to tidal erosion around the plants which have colonised the flats, and of channels caused by the slow drainage of the softer surface mud, are characteristic of the environment. The river water which inundates the vegetation contains 2–3 per cent. of chlorides reckoned as NaCl and is slightly alkaline, the Humber having a chalk bed in places.

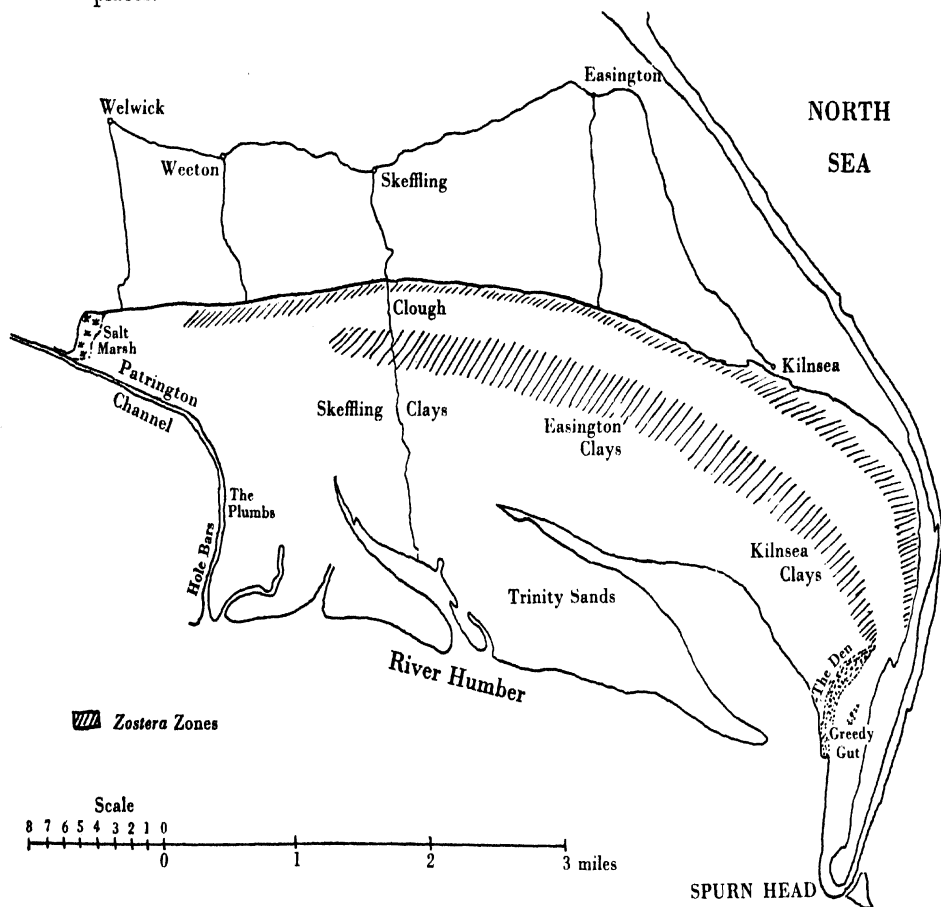


FIG. 1. Sketch map of area.

About 1–2 ft. below the surface of the sandy silt there is a comparatively firm black mud, in which decaying organic matter and plant remains are being assisted in putrefaction by anaerobic bacteria producing hydrogen sulphide. As sulphur bacteria (*Beggiatoa* sp.) occur elsewhere in the Humber tidal pools, it is possible that they are also responsible here for the conversion of hydrogen sulphide into sulphates. Another feature of the Humber bacterial flora is the occurrence of iron bacteria, and the black colour of the substratum is probably

due to ferrous sulphide thrown down from iron compounds by the hydrogen sulphide generated by putrefactive bacteria. That this is an important cycle in the chemistry of the environment there seems little doubt. It is obvious also that the sewage pollution of the river water must contribute to the supply of organic nitrogen, some of which is available for plant life.

#### CHEMICAL FACTORS LIMITING DISTRIBUTION

The consistency of the surface mud and its content of organic matter appeared superficially to be the limiting factors in the distribution of enalid plants. The following analyses of average surface mud samples tend to confirm these conceptions:

		<i>Zostera</i>	No <i>Zostera</i>
Kilnsea:	pH	—	7.1
	Plasticity	0.0052	0.0056
Easington:	Character	Less sandy	More sandy
	pH	7.3	7.1
	Plasticity	0.0048	0.0048
	Organic matter %	6.7	4.0
	Nitrogen %	1.09	0.65
	Inorganic residue (extracted by hot HNO <sub>3</sub> ) %	80.9	86.4
	Chlorides (as NaCl) %	7.12	5.02
Weeton:	pH	7.3	7.1
	Plasticity	0.0053	0.0056
Paull (out of the area where plants occur):	pH	—	7.5
	Plasticity	—	0.0056

The figures given for plasticity are the number of grams of normal sodium carbonate absorbed by 1 gm. of dry mud. This chemical estimation of consistency is not absolutely satisfactory, as at Easington there was a visible difference between mud from the bare ground and mud from the plant zone. Roughly stated the consistency varies from hard ripple-marked sand, to soft mud into which one sinks up to the ankles. At Weeton and Easington the mud appears more alkaline in the plant zones.

At Easington there is a marked difference in the amount of nitrogen; this was estimated by Kjeldahl's method and is not all necessarily "available". It is interesting to compare the nitrogen content of the mud above Hull (0.14–0.21 per cent.), obtained at Redcliff Sand by Good and Waugh (1934), with the Easington figures; sewage pollution may account for the greater fertility of the Easington clays. The amount of chlorides in the mud is remarkably high, being equivalent in the plant zone to an osmotic pressure at 15° C. of 28.72 atmospheres.

#### ENALID PLANT ASSOCIATES

Having defined the main characters of the environment, it is convenient to give a description of the plant association. This consists of three species, the dominant *Zostera marina* L. var. *stenophylla* Aschers. and Graeb., *Z. marina* var. *angustifolia* Horn., and the subdominant *Ruppia rostellata* Koch.

*Zostera marina* L. vars. These plants, commonly known as grass-wrack, eel grass, or widgeon grass, are characteristic plant colonists of soft maritime mud,

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having a creeping rootstock and narrow ribbon-like leaves. The great variation in size of the plants makes identification a matter of difficulty. The leaves of Humber specimens vary in breadth from 1.0 to 3.5 mm. and in length from 4.3 to 45.7 cm. Plants from the following stations were examined: Weeton, Skeffling, Easington, Kilnsea, The Den; the largest plants occurring from Kilnsea towards Spurn on soft mud, and the smallest on the harder sandy ground at Easington and inside Spurn Head. The number of veins in the leaves varies from three to five in the plants observed. The type *Z. marina* L. is an altogether larger plant with longer (up to 1 m.) and broader (4–6 mm.) leaves, occurring in deeper water. Although these Humber inshore forms can be referred to the narrow-leaved var. *angustifolia* Hornem., it was found that the position of the veins of the three-veined plant placed it as var. *stenophylla* Ascherson and Graebner. The latter has one median vein and the two lateral veins are midway between the margin and the mid-rib and parallel throughout their length. The five-veined plants have two veins almost coalescing with the margin, this being consistent with the description of var. *angustifolia* Hornem.; this variety is not so common as var. *stenophylla*. The latter flowers and fruits in the Humber, the flowers appearing in July and the seeds ripening towards the end of August. The seeds are longitudinally striated and white to brown in colour. Propagation is probably supplemented by fragments of the rhizomes broken loose in heavy weather. Among the material collected no plants appeared to belong to *Zostera nana* Roth., as none had one-veined leaves, and sections of the stem revealed the cortical bundles in the outermost layer of the cortex, not in the inner layer as in *Z. nana*.

*Ruppia rostellata* Koch. This is a very delicate plant with a creeping rootstock and narrow one-veined ribbon-like leaves. It has not yet been found flowering by the writer, and was at first confused with *Zostera nana* owing to the similarity in vegetative characters. But consideration of the general morphology and the internal anatomy of the stem identified it with *Ruppia rostellata* Koch. Plants have been found in Patrington Haven, at Easington and from Kilnsea to Spurn. Owing to the tidal rise and fall at these places there would be some difficulty for *Ruppia* to flower except under water as does *Zostera*; one would not expect to find the long peduncle of *Ruppia maritima* L. where the short peduncle of *R. rostellata* is more adapted to the environment. At Easington and from Kilnsea to Spurn, *Ruppia* appears more resistant to desiccation than *Zostera*, not occurring in pools but on drained ridges; in Patrington Haven it is submerged even at low tide and subject to greater changes in salinity.

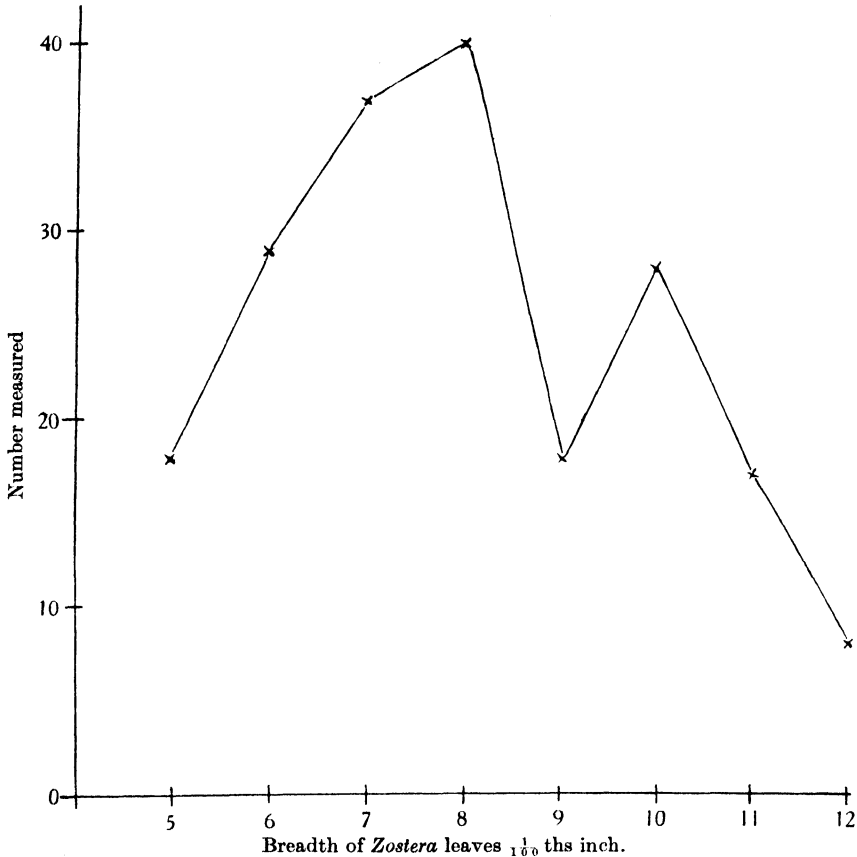
### DISTRIBUTION

*Zostera* occurs in two main zones illustrated on a tracing of the 1-in. ordnance map (Fig. 1) by shading:

**Zone 1.** A shore zone running parallel with the revetment, the plants existing at low tide in shallow circular pools on a mud of medium consistency.

**Zone 2.** Here the plants appear more healthy in a wide zone in fairly deep channels on the softest mud.

Between these two main zones on harder sandy ground sporadic plants of *Ruppia* and the smaller forms of *Zostera* occur in places; where the ground is hardest, as at Weeton, the ground is bare of phanerogams. During the last 30 years the *Zostera* has, if anything, extended from Skeffling in the direction of



GRAPH 1. Two races of *Zostera* reflected in the breadth variation.

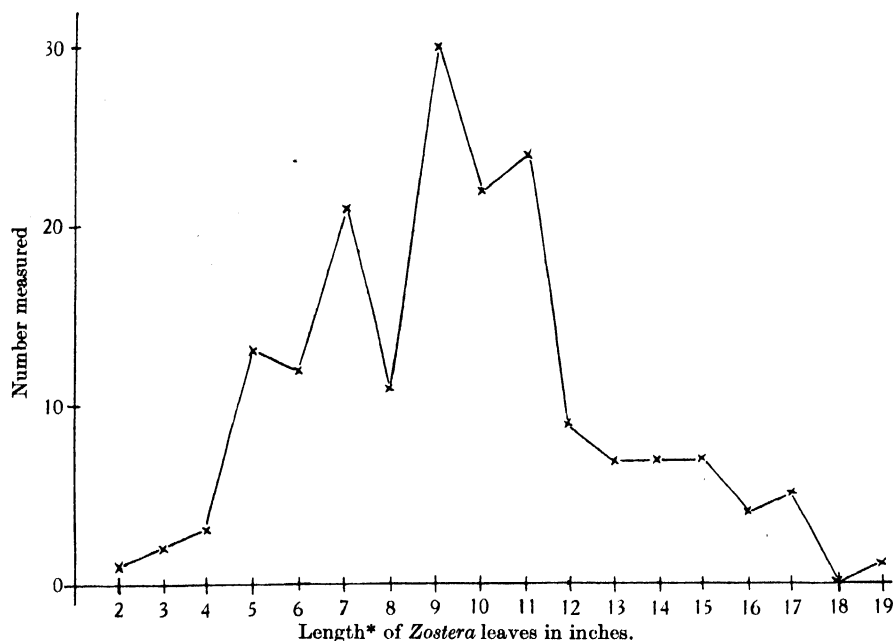
Weeton, where it is now mainly limited by hard sands on the east of Patrington channel (Welwick). Near the Den, *Zostera* is limited by hard sands and the raised stony beds of *Mytilus edulis*. The great turbidity of Humber water is no doubt the factor limiting the extent of zone 2 and the distribution in deeper water, as well as the fact that the mud becomes softer towards low tide mark. *Ruppia* occurs mixed with the *Zostera* at Easington and from Kilnsea towards Spurn: it is sporadic rather than uncommon at present. Some algae contribute to the mixed plant association from Kilnsea to the Den. A diagram is included,

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approximately to scale, showing the lateral zonation of plants in a series of transverse sectors at different points (see Fig. 4, p. 214).

### VARIATION AND GROWTH OF *ZOSTERA* LEAVES

The variation in size of *Zostera* plants was particularly noticeable at Easington. In an attempt to differentiate the Humber forms measurements were made of about 200 leaves from plants collected at random between tide marks. Three methods of plotting these results give interesting graphs: (i) the breadth against the number having a given breadth, (ii) the length against the number having a given length, and (iii) the growth gradient of the leaves. In



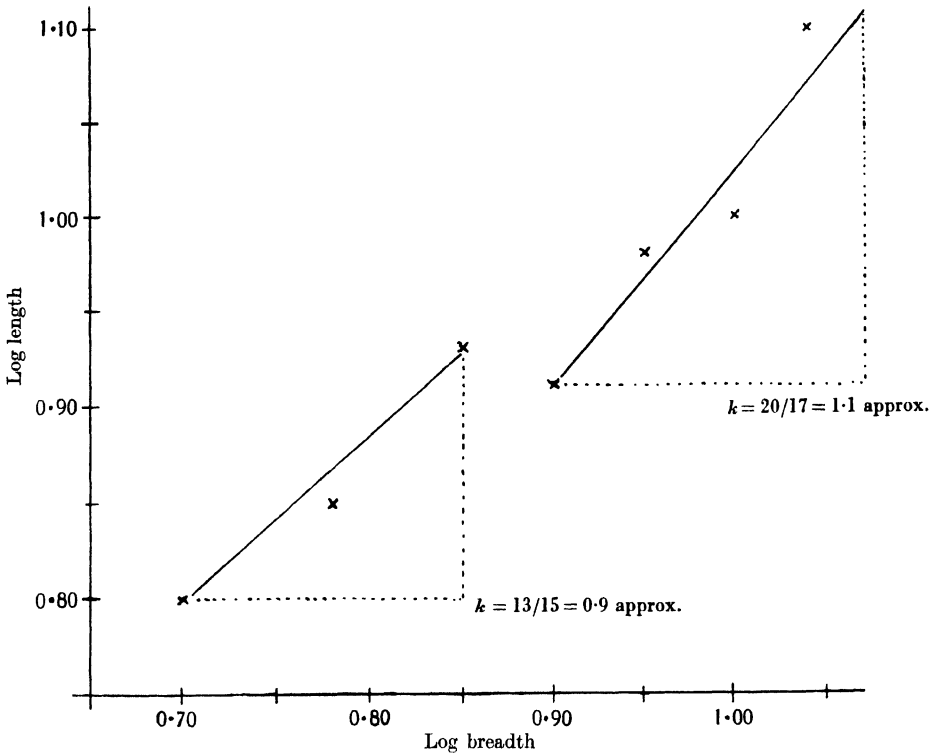
GRAPH 2. Two races of *Zostera* reflected in the length variation.

\* Note length 2 includes leaves between 1 and 2 in.; length 3 leaves between 2 and 3 in., and so on.

the last use was made of Huxley's (1932) simple heterogony formula ( $y = bx^k$ ), the length being plotted against the breadth on a double logarithmic grid. In each of the three graphs two forms or races of *Zostera* are indicated. The two growth gradients of the leaves are especially remarkable: the broader leaved more healthy plants colonising the softest mud having a growth coefficient of  $k = 1.1$ , and the narrower leaved form in pools and on more solid ground a growth coefficient of  $k = 0.9$ . It was necessary to take an average length for each breadth; the breadths were measured to the nearest hundredth of an inch.

These results agree with those obtained by Ostenfeld in Danish waters, in spite of the fact that both the "narrow-leaved sand *Zostera*" and the "broad-leaved mud *Zostera*" studied there were larger plants occurring in deeper water.

*Zostera* is a plant that is green all the year round, and the periodicity in the growth of the leaves was demonstrated by Ostenfeld, whose figures, when presented in graph form, show clearly that the summer leaves are longer and broader than the winter leaves. The measurement of Humber plants was carried out in autumn, and owing to the inner leaves being younger than the outer, leaves in various stages of growth will have been obtained. It is interesting to find that the two ecological types defined by Ostenfeld have analogues



GRAPH 3. Growth gradients of *Zostera* leaves, length plotted against breadth on a double logarithmic grid.

in these smaller inshore forms, and this lays emphasis on the importance of the nature of the substratum. Furthermore, taken together with the nitrogen content of the mud, this may account for the "nanism" of the plant and consequent difficulty in differentiating the described varieties. It seems in the light of these results that the two forms of *Zostera* having different growth coefficients may either be the same as the varieties *stenophylla* and *angustifolia*, or may be local races determined by the far from uniform environment. It is evident that the two main varieties occur with many local variations.

## MORPHOLOGY OF ENALID PLANTS

Although the adaptations to environment of such a specialised vegetation may be only inferred from its morphology and anatomy, this is of interest from an ecological standpoint. Before considering these adaptations some description of structure will therefore be given.

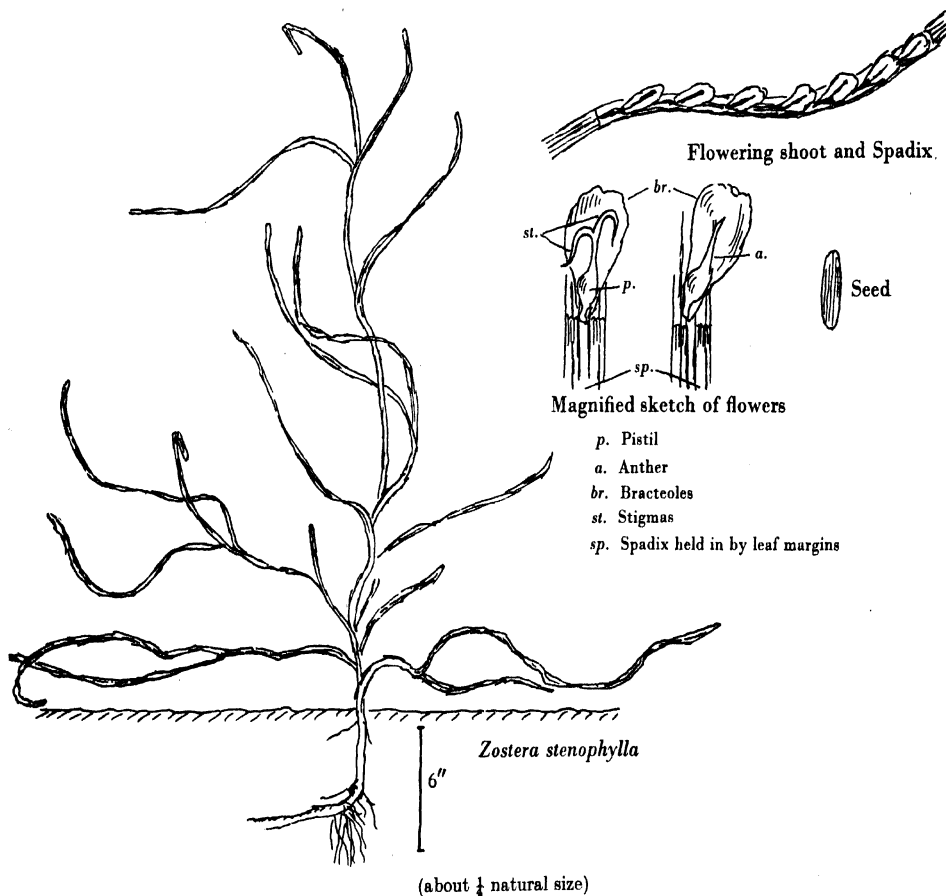
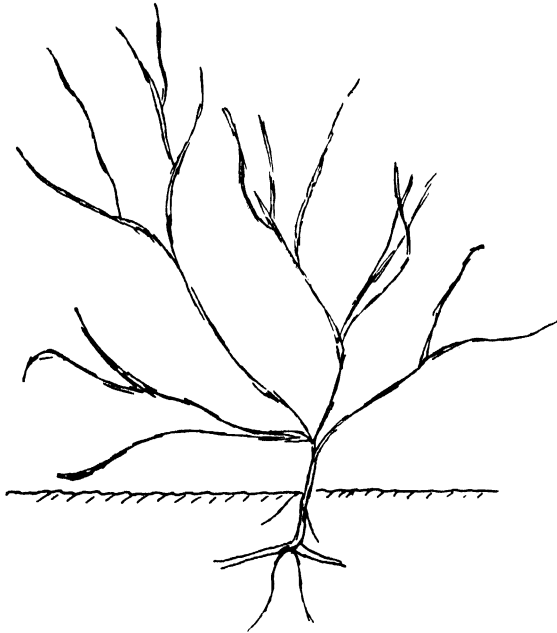


FIG. 2. Diagrams of vegetative and floral characters of Humber *Zostera*.

(1) *Root systems*. The plants are pioneers of soft mud, which is relatively more obstinate to colonisation than firm mud, first because it is not easy for many otherwise suitable species to get a proper foothold, and secondly because its waterlogged state retards the diffusion of oxygen needed by the embedded parts of the plant. *Zostera* and *Ruppia* are specialised to deal with this peculiar habitat, a firm anchorage being provided by a creeping rhizome rooting at the nodes. The rhizomes are at a depth of about 6 in. (see Figs. 2 and 3). Both



*Ruppia rostellata* (about  $\frac{1}{3}$  natural size)

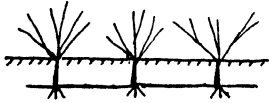
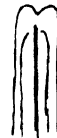
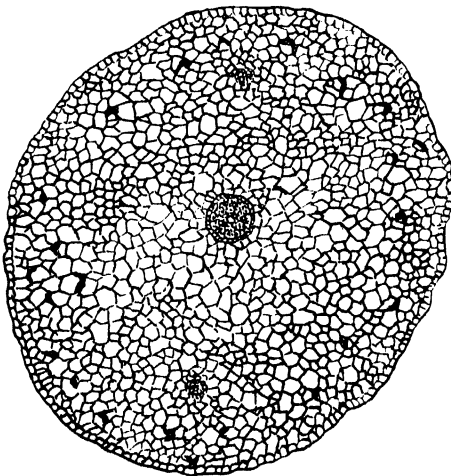


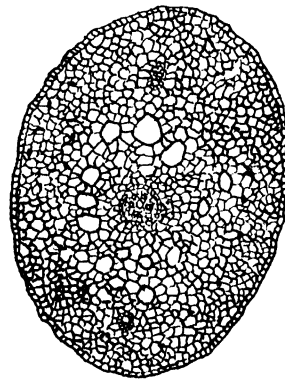
Diagram showing creeping rhizome of  
*Zostera* and *Ruppia*



Tip of leaf in *Ruppia*



*Zostera* stem ( $\times 82$ )



*Ruppia* stem ( $\times 82$ )

Transverse sections of stems above ground.

FIG. 3. Vegetative characters of *Ruppia*, and comparative anatomy of ensalid stems.



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plants are perennial, the aerial shoots dying down each year, the majority of the leaves being shed in autumn. Growth is carried on by a lateral bud from

WEETON	SKEFFLING	EASINGTON	KILNSEA	MIDDLE OF SPURN PENINSULA	NEAR THE DEN
— Mud	== Algae — Soft mud	— Soft mud	== Shingle == Algae	— Shingle — Algae	== Shingle == Algae
<i>Zostera</i> pools	<i>Zostera</i> —	<i>Zostera</i> pools <i>Ruppia</i> sporadic —	<i>Zostera</i> sporadic. Stony channelled silt <i>Enteromorpha</i> <i>Zostera</i> pools. Hard stony silt <i>Ruppia</i> on margins. Coarse reddish sand	<i>Zostera</i> <i>Ruppia</i> . Soft silt — <i>Ruppia</i> . Hard ground <i>Zostera</i> pools. <i>Fucus</i> on post — <i>Zostera</i> sporadic —	<i>Zostera</i> <i>Ruppia</i> — Sandy ground — <i>Zostera</i> Soft mud —
—  Hard sands	Sandy mud  —  <i>Zostera</i> in channels  Soft mud  —	Hard sandy ground  <i>Zostera</i> occasional  <i>Ruppia</i>  —  Soft channelled mud  <i>Zostera</i>  —	Ripple marked sands  <i>Zostera</i> sparse  <i>Rhizoclonium</i>  —  <i>Zostera</i>  Soft mud  —	Hard sand  —  <i>Zostera</i>  Soft mud  —	—  <i>Zostera</i> Soft mud  —

BANK  
↑  
↓  
RIVER  
HUMBER

FIG. 4. Transverse sectors of plant zones (scale approx. 1 mm. = 10 yards).

the base, which first extends horizontally for a variable distance and then bends up to the light. The new shaft thus formed roots freely at the base: in *Zostera* a cluster of branchless white roots occurs at the nodes, only one or two roots being present in the more delicate *Ruppia*. The actual plant of any year is a rooted branch of last year's plant. It is also necessary in this environment for

seedlings to establish their roots rapidly in the more stable subsoil owing to the mobility of the surface mud under the action of tidal currents.

The dense plexus of creeping rhizomes tend gradually to consolidate the mud, and where this has happened (e.g. at Southampton), the sea-grass vegetation has been succeeded by *Salicornia* and *Spartina*. The possibility of this succession in the future on the Humber flats is not so very remote, as the salt marsh at Welwick (see map) has an outpost zone of *Salicornia herbacea* L. and a planted patch of *Spartina Townsendii* Groves, which are both thriving at the moment. In both *Zostera* and *Ruppia* there is a coleorrhiza or root sheath, which protects the young root at the commencement of growth.

(2) *Leaves*. The leaves of the two plants are similar in some respects. They are placed on the horizontal creeping rootstock, each leaf consisting of a lower tubular sheath and a long flat ribbon-like blade. In *Ruppia* the sheaths are comparatively short and vegetative scale leaves clothe the base of the axillary structure. The sheaths of *Zostera* give the rootstock a nodose appearance, forming a ridge where the leaves arise. The older leaves have a space of 1–2 cm. between them, but towards the end of the shoot the internodes are very short where the shoot is growing. Near each leaf occur the beginnings of side shoots—small buds peculiarly placed, not in the axil, but above the base of the sheath; some of these may develop into independent branching shoots. In *Zostera* the main leaf veins are connected in places by cross-fibres at right angles. Both plants possess extremely tough and flexible leaves, those of *Ruppia* having an indented tip (Fig. 3) and the *Zostera* leaves being rounded.

(3) *Flowering shoots*. The flower-bearing shoots of *Zostera* do not reach full development until late summer. The tip of the rootstock becomes the flower-bearing shoot, the internodes growing larger and no roots appearing at the nodes. The rather terete stem becomes flattened and the leaves become shorter; ramification gives the flowering shoots a sympodial character. The flowers themselves appear on a flat spadix, as in a slit in the leaves. The number of the leaves containing flowers on one plant varied from one to twelve. The flowering shoots only last a few months and in late summer bear inflorescences in all stages of development, a serial flowering taking place.

(4) *Flowers*. The small flowers, devoid of a perianth, are borne on a spadix (5–6 cm. long) held in by folds of the leaf. They consist of a row, alternately anthers and pistils, the latter having two long filiform stigmas. The anthers and pistils are protected, partly by the marginal folds of the leaf slit and by small hood-shaped bracteoles (see Fig. 2). The pollen is unique, being filamentous and devoid of an outer coat or extine. Individual filaments measured  $2.8\mu$  by about  $1000\mu$ : the nucleus could be seen in stained filaments. Fertilisation is hydrophilous, and this is said to be peculiar to *Zostera* alone among British plants; but *Ruppia rostellata* is probably also pollinated by the agency of water. The number of individual flowers along the length of the *Zostera* spadix varied from five to ten.

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(5) *Internal anatomy.* The chief anatomical characters of the stem in *Zostera* and *Ruppia* are the following:

- (i) Thin-walled epidermis.
- (ii) Loosely constructed cortex.
- (iii) Radially arranged lacunae—comparatively large in *Ruppia*.
- (iv) Two small cortical bundles: in *Ruppia* there are fibrovascular connections with the leaf sheaths, in *Zostera* the bundles are continuous up and down the cortex, sending a branch to the central cylinder at the nodes.
- (v) Well-defined endodermis.
- (vi) Very simple axial vascular region of concentric structure.
- (vii) Reduced sclerenchymatous cells radially arranged in the outer cortex (see comparison, Fig. 3).

The leaf sections reveal the vascular bundles, lacunae and the dense mass of epidermal cells containing chloroplasts; stomates are absent. The leaf tip of *Ruppia rostellata* does not appear to possess marginal teeth as does that of *R. maritima*. The chief character of the roots is the reduction of the xylem area to a few rudimentary tracheae, and the total lack of branching of these very slender organs.

### ADAPTATION TO ENVIRONMENT

The Enalid or sea-grass vegetation may be considered as both hydrophyte and halophyte. The plants exhibit formal, structural and physiological adjustments to both an aquatic and a saline environment.

(a) *Hydrophytic features.* Externally the shoots have a wide-spreading branch system with slender stems and long supple grass-like leaves, whose length gives a good photosynthetic surface and whose narrowness offers a minimum resistance to tidal currents. There is a thin-walled epidermis, a lack of effective mechanical tissue, and a reduction of the vascular system. The sheathing stipules protect axillary structures and strengthen the attachment to the stem. The internal lacunae allow the oxygen dissociated from carbon dioxide in photosynthesis to diffuse readily to the rhizomes and roots. A certain amount of air in the leaf lacunae keeps the leaves floating off the mud. As in other hydrophytes there is reduction of the root system as compared with land plants, corresponding with its reduced importance. In *Ruppia* and *Zostera* it is represented only by small unbranched adventitious roots borne at the nodes. Also the numerous lacunae and the reduction of the vascular system of the roots are characteristic features of water plants.

(b) *Halophytic features.* Both plants show remarkable adaptation in their power to live and reproduce in salt water, which if applied to submerged fresh-water plants causes immediate plasmolysis. The halophytes are distinguished from other plants by the high salt concentrations of their sap, and these concentrations are found to vary according to the rise or fall in the salinity of the environment. These adjustments are rapidly effected; it is also stated that

halophytes possess the power of decomposing chlorides and rendering them innocuous. The plants under consideration may possibly have this power as the rhizomes are under an osmotic pressure of 28.72 atmospheres at 15° C., whilst the leaves in sea water are only under a pressure of 12.12 atmospheres at the same temperature, until there is equilibrium set up between the water and the surface soil. The absorption of water from salt solutions is slow and difficult, and in land halophytes typical xeromorphic characters, such as succulence, reduction of stomates, etc., are found. Transpiration as such does not appear in *Zostera* and *Ruppia*. The comparatively small amount of water absorbed by the roots, the absence of any openings in the leaf through which water could pass, moreover the fact that the epidermal cells of the leaves are practically all photosynthetic, absorbing solutions from the outside into the interior, indicate the giving off of a very small amount of water, if any, from the leaves. It is probable that waste gases can pass out in solution through the cell walls, but structures adapted for the retention of a water supply and reduction of transpiration are unnecessary in *Zostera* and *Ruppia*. The modification of the reproductive system for flowering and pollination under water, rather reminiscent of the reproduction of algae, is perhaps the most remarkable of all the specialisations of these most interesting plants.

#### THE ALGAE OF THE AREA

To assist further in characterising the environment the inclusion of a superficial survey of algae of the area may be useful. Although the alga flora of the Humber estuary is sparse a few species are "silt binders" accessory to the flowering plants described. These are of two types: (i) those associated with the flowering plants, and having branching rhizoids rooting in the mud, forming a matted network of filaments; and (ii) those that form thin films on the surface of the mud flats, possibly stabilising the surface to some extent. Two other types that are not important in land reclamation are (iii) algae attached to stones and woodwork, and (iv) epiphytic algae. The ecological significance of the algae in the Humber is evident if not important; their role is one of helping the accretion of silt and they are undoubtedly pioneers on the very softest mud. The branched forms make nets for the floating seeds of phanerogams and may protect the young seedlings. As epiphytes they may endanger the life of *Zostera*, as their abundance limits the photosynthetic surface of the leaves.

PHAEOPHYCEAE: No fucoids have been found in the salt marsh at Welwick, as it is now too well established to support them. *Fucus vesiculosus* L. occurs on the artificial chalk stone "cranches" and embankments as at Welwick, Weeton, Skeffling, Kilnsea, and on the stony mussel beds of the Den; several wooden posts on the mud flats also bear growths of this species. At Patrington channel mouth the dwarfing and reduction of the bladders owing to the in-

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fluence of fresh water can be observed. *Phyllitis fascia* Kütz. occurs on the Den associated with *Fucus*.

**RHODOPHYCEAE:** *Porphyra vulgaris* Ag., *Corallina officinalis* L., and *Chondrus crispus* Lyngb. were all first recorded by Petch on the Den: the last is now abundant. *Cruoria pellita* Lyngb. covers the chalk blocks of a breakwater on the mud flats at Welwick.

**CHLOROPHYCEAE:** These algae cover the largest amount of ground and are of most economic importance, as they alone are silt binders. *Vaucheria dichotoma* Lyngb. var. *submarina* Ag. forms dense mats of filaments on the saltmarsh at Welwick. *Enteromorpha prolifera* Ag. is dominant in the saltmarsh pools at Welwick and associated with *Zostera* in pools near Kilnsea. *Rhizoclonium pachydermum* Kjellm. occurs in salt-marsh pools and on hard sandy flats at Welwick and near the Den. *Ulva lactuca* L. occurs on the Den, and at Kilnsea, Skeffling, Weeton, and Welwick. It varies considerably, one variety being epiphytic on the roots of phanerogams in the salt marsh and another attached to stones on the Den. *Enteromorpha compressa* Grev. occurs on stones on the margins of the mud flats at Welwick, Skeffling, Kilnsea and Spurn. It is very variable in size and amount of branching. *Monostroma zostericolum* Tilden is epiphytic on *Zostera* at Weeton.

**FLAGELLATA:** *Euglena limosa* Gard. forms an apple green film on the soft surface mud in the outer *Zostera* zone near Kilnsea.

**DIATOMACEAE:** The following occur as epiphytes on *Zostera*: *Cocconeis distans* (Grev.) Grun. almost covering the leaves in places; *Berkeleya obtusa* Grev., a form having the frustules packed in mucus tubes.

The following are epiphytes on other algae, especially *Enteromorpha* and *Rhizoclonium*: *Achnanthes brevipes* var. *minor*, *A. coarctata* Bréb., *Cocconeis scutellum* Ehr., *Rhoicosphenia curvata* var. *marina*, *Epithemia Musculus* Kütz.

In pools and forming films on the mud flats are: *Actinopterychus undulatus* Ehr., *Coscinodiscus centralis* Ehr., *C. radiatus* Ehr., *C. subtilis* (Ehr.) Grun., *Melosira sulcata* (Ehr.) Kütz., *Rhaphoneis amphiceros* Ehr., *Pleurosigma balticum* W.Sm.

Many other species occur, but sufficient indication of the most important algae has been given.

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## REFERENCES

- Butcher, R. W.** Report on *Zostera*, Ministry of Agriculture, Dec. 1933.
- Carey, A. E. and Oliver, F. W.** *Tidal Lands*, London, 1918.
- Carter, N.** "Alga flora of two saltmarshes." *This JOURN.* **21**, 1933.
- Collins, F. S.** *Green Algae of North America*. Tufts Coll. Stud. II, No. 3, July 1909.
- Druce, G. C.** *Hayward's Botanists' Pocket-book*, 19th ed., London, 1930.
- Good, R. D'O. and Waugh, W. L.** "The vegetation of Redcliff sand; a contribution to the ecology of the Humber." *This JOURN.* **22**, 1934.
- Groves, A. H.** "The morphology of *Ruppia maritima*." *Trans. Conn. Acad. Arts Sci.*, **14**, 1908.
- Huxley, J. S.** *Problems of Relative Growth*, London, 1932.
- Newton, L.** *Handbook of the British Seaweeds*, Brit. Museum, 1931.
- Ostenfeld, C. H.** "The ecology and distribution of *Zostera marina* in Danish waters." *Rep. Danish Biol. Sta.* **16**, 1908.
- Petch, T.** "Marine fauna of the Humber district." *Trans. Hull Sci. Fld Nat. Cl.* **3**, 27, 1903; *Yorks. Nat. Union Spurn circular* July, 1904.
- Philip, R. H.** "Diatomaceae of Hull and District." *Trans. Hull Sci. Fld Nat. Cl.* **1**, pt. iv, 1901.
- Robinson, J. F.** "Flora of the East Riding of Yorkshire." *Trans. Hull Sci. Fld Nat. Cl.* **2**, 1902.

# IRRIGATION EXPERIMENTS ON A SCOTTISH HILL PASTURE

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IN a paper on experiments in the improvement of hill pasture in Midlothian (Heddle and Ogg, 1933) attention was drawn to the close relationship existing between the distribution of the better types of grazing herbage and the presence of spring water at or near the surface. Those areas which are subject to natural irrigation or "flushing" by spring water are at once the most productive and, if drainage is efficient, the most palatable to stock. They carry a characteristic herbage with considerable quantities of *Agrostis* spp., *Holcus lanatus*, *Festuca rubra*, *Trifolium repens* and other species of comparatively high grazing value, and they respond better to applications of phosphatic manures than any of the other herbage types studied.

This association between the presence of spring water and pasture of superior value suggests the possibility of improving the grazing value of hill ground by artificial irrigation of parts which are not subject to flushing in the ordinary course of events. This is indeed a practice of some antiquity, and references to it are to be found in agricultural writings of more than a century ago (Robertson, 1799; Robie, 1876; Smith, 1799). Even at that time the practice seems to have been an old one, for Robertson in 1799 states that it was more frequent in the past and recommends its wider use.

From a more purely ecological viewpoint the influence of surface flushing in affecting vegetation has been recognised for some time. Crampton (1911) described the effect of springs on the moorland vegetation of Caithness, distinguishing "wet flushes" with a permanently wet surface, and "dry flushes" where the flow of water is only intermittent. He also stressed the importance of the nature and source of the water, distinguishing between acid flushes, where the water was derived directly from acid peat and the underlying leached rock and was poor in lime, and calcareous flushes in which the water contained considerable quantities of lime in solution. These different conditions led to differences in the vegetation. Smith and Crampton (1914) recognised that there is a type of natural grassland owing its origin to flushing. One of the sites they enumerate for natural grasslands in this country is "sloping smooth surfaces with a rainwash soil liable to periodical flushing with mineralised waters and rainwash from higher levels". Flush grassland is again expressly recognised by Smith (1918a). He described it as characterised by the presence

of such species as *Festuca ovina*, *Agrostis alba*, *Cynosurus cristatus*, *Holcus lanatus*, *Trifolium repens* and *Ranunculus repens*, and discussed the effect of artificial flushing on Nardetum, as practised in Switzerland. Farrow (1925) described the effect of artificial watering by means of a water drip upon the vegetation of a dry grass heath. He noted a marked increase in the luxuriance of the herbage, and the fact that *Agrostis vulgaris* was strongly encouraged at the expense of *Festuca ovina*. This effect was attributed entirely to the increase in the available water supply.

It was doubtless assumed by many of those who practised irrigation that the improvements were due to the increase in moisture, but here and there we find emphasis laid on the source of the water. Thus Singers (1807) recommends the use of water from marl, i.e. water rich in lime, and states that mossy water from peat bogs is not suitable. Recent investigators of the question have also stressed the importance of the source and nature of the water. Crampton (1911) in discussing the subject says: "...the underlying causes are probably of a complex nature and vary in different cases. The acidity or alkalinity of the waters, the state of aeration and rate of flow, and its constant or periodic nature, would all have to be considered." Smith and Crampton (1914) emphasise the importance of dissolved alkaline bases in the water, as preventing leaching of the surface layers of the soil, and stress the effect of alternate flooding and rapid drainage in ensuring aeration and preventing souring and rapid accumulation of raw humus. The same factors are again referred to by Smith (1918b). Emphasis is thus laid by these writers on the presumed effect on the soil of the bases dissolved in the water. No experimental investigation of this question, however, seems to have been made, and it was in order to study the effects of flushing under controlled conditions upon both vegetation and soil that the experiments described in the present paper were undertaken. The experiments were carried out on the hill pasture of the farm belonging to the Edinburgh and East of Scotland College of Agriculture.

The farm is situated on the south side of the Pentland Hills, five miles south of Edinburgh, and the hill grazing is at an altitude of 900–1600 ft. The average annual rainfall at the farm (at an altitude of 645 ft.) is 36 in., and on the hill land it will be considerably higher.

The rocks over the whole area are volcanic in origin, and may be divided into two main groups, a basic, consisting of basic andesites and basalts, and an acid, consisting of acid andesites, rhyolitic lavas, trachyte and tuff. On the lower ground the rocks are covered by boulder clay and by sands and gravels, but on the higher ground the drift, except in spots, is thin or absent. There are several springs and most of these are on the area of basic rocks.

The pasture is very varied, but most of it is in need of improvement, large areas being covered with *Nardus*, *Calluna*, and short *Festuca-Agrostis* types of vegetation. In general the herbage overlying the basic rocks is superior to that overlying the acid rocks from a grazier's point of view.



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The method adopted for leading the spring water on to the area to be flushed was to cut a shallow ditch from the source of the spring, following, but with a slight fall, the contour of the slope. The water was allowed to flow freely down the slope from the end of the ditch. At convenient intervals of time the ditch was extended by 1 or 2 yards so as to carry the water on to a fresh area of ground, and in this way the flushed area was gradually extended along the slope. The possibility of flushing in this way is naturally limited by the contour of the ground, the distribution of different vegetation types, and the strength and constancy of flow of the spring, but under favourable conditions a considerable area can be flushed.

### ANALYSES OF WATER SAMPLES

On account of the geological differences it was anticipated that there would be a considerable variation in the composition of the water in different parts of the glen. Samples for analysis were taken in May and the results are given in Table I. Four of these were from areas of vegetation listed in Table IV. The electrical conductivity measurements were done by means of a Digby and Biggs Dionic Water Tester.

Table I. *Analysis of water samples from Boghall Glen (expressed as parts per 100,000)*

Vegetation area (cf. Table IV)	Sample No.	Total solids	Calcium as CaO	Magnesium as MgO	Potassium and sodium as KCl and NaCl	Chlorine	Con- ductivity in gemmhos (at 20° C.)
From acidic rocks:							
—	1	4.50	0.37	0.18	1.60	1.08	70
6	2	6.90	0.77	0.52	2.22	1.52	67
—	3	6.10	0.65	0.38	2.00	0.90	70
From basic rocks:							
2	4	10.47	2.28	0.59	3.34	1.29	128
3	5	10.82	2.39	0.39	3.30	1.42	150
4	6	12.37	3.02	0.34	3.27	1.29	160
—	7	12.40	3.35	0.63	2.78	1.38	170
—	8	7.00	3.59	0.76	3.80	1.38	200
—	9	11.20	2.29	—	3.16	1.48	142
—	10	12.30	2.78	0.47	5.00	1.48	165

It is evident from the table that the water samples can be divided into two groups. The first three samples, which come from the area of acid rocks, have a much lower conductivity and also a much lower content of calcium than the others, which are from the area of basic rocks. The figures for sodium and potassium are also considerably lower for the samples from the area of acid rocks. The difference in calcium is particularly striking, the one group containing about four times as much calcium as the other.

The seasonal variations in composition of the water have not been studied, but conductivity measurements have been made at different periods of the year, and some of the typical results are given in Table II.

Table II. *Seasonal variations in electrical conductivity of spring waters, Boghall Glen*

No.	Conductivity in gemmhos (at 20° C.)			
	May	June	Dec.	Jan.
From basic rocks:				
1	110	125	135	—
2	—	280	230	—
3	145	150	—	123
4	150	145	140	110
5	160	180	160	—
6	175	180	—	145
7	175	170	160	142
8	157	160	145	135
9	—	128	140	—
10	153	—	170	—
11	—	175	145	—
12	—	190	165	—
13	—	210	190	—
From acidic rocks:				
14	63	—	90	83
15	48	78	93	82
16	—	—	82	75
17	—	—	88	78
18	—	—	—	80
19	—	—	—	80
20	—	—	—	77

There is a considerable seasonal variation in the conductivity of the water from different sources, but the figures for the two groups of springs remain distinct, those from the basic rock area giving constantly higher figures than those from the acid rock area. Thus in no case has the conductivity recorded for the basic springs fallen below 100, and it is generally over 140 and may attain levels as high as 280, while the acidic springs have never shown conductivities of more than 100 and frequently fall considerably below this level. There is some difficulty in obtaining samples during summer, especially from the acidic springs, as they frequently dry up.

#### METHODS OF SAMPLING AND ANALYSIS OF SOIL AND HERBAGE

Soil samples were taken from five different areas where flushing experiments were carried out. Sampling was done by means of an auger to a depth of 8 in., and each sample consisted of at least fifteen separate auger borings. The pH measurements were done by means of the quinhydrone electrode (*Rep. Second Internat. Com. for Soil Research*, 1930) and the amounts of CaO required to bring samples to pH 6, 6.5 and 7 were determined by the modification of Remesow's neutralisation curve method suggested by Smith and Coull (1932). Exchangeable calcium was determined by extraction with ammonium acetate (Schollenberger and Dreibelbis, 1930). Readily soluble potash was estimated by shaking 20 gm. of soil and 800 c.c. of 0.5 *N* acetic acid in an "end-over-end" shaker for 6 hours and determining the potash in the extract by the cobaltinitrite method. Readily soluble phosphoric acid was

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estimated by Kirsanov's method (1932), 5 gm. of soil and 25 c.c. of 0.2N hydrochloric acid being shaken for 5 min., allowed to stand for 15 min. and the phosphoric acid estimated colorimetrically.

The samples from the unflushed portions were taken from areas immediately adjoining the flushed, and the soil profiles were carefully examined to ensure as far as possible that there was no difference in soil type. The results of the soil analyses are given in Table III.

Table III. *Chemical analyses of soil samples from flushed and unflushed areas, Boghall Glen*

Sample No.	Vegetation area (cf. Table IV)	Flushed (F.) or unflushed (U.)	pH	Exchange-able calcium as % CaO	Percentage CaO required to bring soil to pH			Readily soluble K <sub>2</sub> O mg. per 100 gm.	Readily soluble P <sub>2</sub> O <sub>5</sub> mg. per 100 gm.	Loss on ignition %
					6.0	6.5	7.0			
1	2	U.	4.66	0.14	0.25	0.35	0.45	20	33	13.7
2	2	F.	6.00	0.24	0.00	0.07	0.15	13	21	12.4
3	3	U.	4.31	0.04	0.35	0.44	0.52	12	4	13.7
4	3	F.	6.09	0.32	0.00	0.05	0.13	15	3	13.8
5	3	U.	4.50	0.03	0.33	0.43	0.53	14	5	13.1
6	3	F.	5.36	0.17	0.10	0.19	0.29	13	4	13.0
7	3	F.	5.57	0.12	0.06	0.14	0.27	14	2	12.9
8	3	U.	4.35	0.05	0.38	0.47	0.52	12	3	12.2
9	3	F.	5.70	0.26	0.04	0.10	0.18	13	3	15.1
10	3	F.	5.64	0.20	0.04	0.13	0.32	15	2	14.7
11	4	U.	4.39	0.03	0.45	—	—	19	3	20.0
12	4	F.	5.27	0.27	0.05	0.12	0.25	11	2	15.0
13	5	U.	5.13	0.37	0.08	0.15	0.24	10	2	16.5
14	5	F.	5.65	0.46	0.02	0.06	0.12	9	3	15.1
15	6	U.	4.25	0.04	0.51	0.57	—	15	4	21.2
16	6	F.	4.92	0.08	0.27	0.38	0.48	11	3	14.4

Botanical analyses were made by the percentage frequency method (Robinson, 1933), at least ten and generally twenty turves, each 6 by 2 in. in size being lifted from each area examined and separated into their constituent species in the laboratory. The results are given in Table IV.

### THE INFLUENCE OF ARTIFICIAL FLUSHING ON SOIL AND VEGETATION

*Area 1.* The vegetation of this area is dominated by *Agrostis tenuis* and *Festuca ovina* with abundance of *Galium saxatile*, a type of herbage associated at Boghall with a soil consisting of a greyish brown, gritty, light loam, powdery and full of grass roots, below which occurs a brown, pervious, gravelly, sandy loam overlying sand and gravel. No soil or water analyses are available for this area.

The effect of flushing on the herbage has been to increase *Agrostis* and *Festuca rubra* to a marked extent and to reduce *Festuca ovina* and *Galium saxatile* considerably.

*Area 2.* This area carries a somewhat similar herbage to the last, and is associated with a similar soil type. The soil analyses for this area are given in Table III, Nos. 1 and 2, and the composition of the irrigation water in Table I, No. 4. There are traces of former cultivation at this spot, and this may account for the high phosphate content of the soil as compared with the other areas.

The effect on the soil has been a marked rise in  $pH$ , and a considerable increase in the exchangeable calcium. There are indications of considerable leaching of readily soluble phosphate and potash in the flushed area. The vegetation shows an increase in *Festuca rubra*, *Holcus lanatus*, *Poa trivialis* and *Trifolium repens*, with reduction of *Festuca ovina* and *Galium saxatile*.

*Area 3.* The herbage of this area was again of a generally similar type to Nos. 1 and 2, but was being invaded by *Nardus stricta* to an appreciable extent and was in consequence being in some degree neglected by the sheep. Soil analyses are given in Table III, Nos. 3–10, and the composition of the water in Table I, No. 5. The soil in this area was similar in appearance to that in area 2, but contained much smaller amounts of exchangeable calcium and readily soluble phosphate.

The effect of flushing on the soil has been to increase the  $pH$  and the exchangeable calcium very markedly, and to decrease the amount of calcium required to bring the  $pH$  to a definite figure. The differences in readily soluble phosphate and potash between the unflushed and flushed areas are not great enough to be significant. The vegetation of this area shows an increase in *Agrostis* and *Festuca rubra* and a reduction in *Festuca ovina* and *Galium saxatile* as a result of flushing.

*Area 4.* The vegetation here is of a different type from that of the previous three examples. In this case *Vaccinium myrtillus* shares dominance with fine-leaved grasses—*Agrostis* spp., *Festuca ovina* and *Deschampsia flexuosa*. The soil has a thin, well-decomposed, peaty surface layer, overlying a dark brown, silty layer which passes into a reddish brown, gravelly, pervious loam. Below this lies a dark, reddish brown, gravelly mass full of rock fragments. Soil data are given in Table III, Nos. 11 and 12, and the analysis of the irrigation water in Table I, No. 6. The figures for exchangeable calcium and readily soluble phosphate in the unflushed soil are again very low, being of somewhat the same order as in area 3.

The effect on the soil of flushing with spring water is similar to that seen in area 3, a marked rise in  $pH$  and exchangeable calcium being recorded. The difference in the content of readily soluble potash between the flushed and unflushed areas is probably associated with the different contents of organic matter (cf. loss on ignition figures), but there may have been some washing out of potash. The herbage shows a marked increase in *Agrostis* spp. and *Festuca rubra* and a reduction of *Festuca ovina*, *Deschampsia flexuosa*, *Galium saxatile* and *Vaccinium myrtillus*.

*Area 5.* This area, although situated not far from area 4, was subject to a certain amount of natural flushing, and the effect of this is seen in the soil analysis figures (Table III, Nos. 13 and 14). No analysis of the irrigation water has been carried out, but conductivity measurements have been made at four periods of the year, and the figures obtained have been constantly somewhat higher than those of the irrigation water used in area 4.

The lime status of the soil before flushing was carried out was considerably better than in the other cases, as may be seen from the *pH*, exchangeable calcium, and neutralisation curve figures. Flushing, however, has effected a further improvement, the *pH* being raised from 5.13 to 5.65, and the exchangeable calcium from 0.37 per cent. CaO to 0.46 per cent. CaO.

The influence of natural flushing on the vegetation can be seen by comparison with area 4, the absence or scarcity of *Vaccinium myrtillus*, *Deschampsia flexuosa* and *Galium saxatile*, and the increased percentages of grasses being noteworthy. The effect of artificial flushing has been to increase *Agrostis* spp. and *Festuca rubra* at the expense of *F. ovina*. *Trifolium repens* also appears to have been slightly favoured by flushing.

*Area 6.* This is again a different vegetation type, in which *Nardus stricta* and *Vaccinium myrtillus* share dominance, the principal associated species being *Festuca ovina* with a certain amount of *Agrostis* spp., chiefly *A. canina*. The soil has a peaty surface layer, high in organic matter, passing into a grey-brown loam and then into a yellowish, gritty and stony loam, with a substratum of reddish, stony boulder clay. Soil analyses are given in Table III, Nos. 15 and 16, and the water analysis in Table I, No. 2. The low *pH*, low content of exchangeable calcium, and large quantity of CaO required to bring the soil to a definite *pH* are noteworthy features. The irrigation water is distinctly less rich in dissolved calcium than that in the other irrigated areas, and this is reflected in the results of flushing. The *pH* rises from 4.25 to 4.92 and the exchangeable calcium from 0.04 to 0.08, but the rise in both cases is small compared with those from some of the other flushed areas. The difference between the loss on ignition figures in the two samples is considerable, and no conclusions can be drawn regarding removal of readily soluble phosphate or potash.

The vegetation of this area shows a striking alteration as a result of flushing. *Agrostis* spp. and *Holcus lanatus* are much increased and *Anthoxanthum odoratum* also shows an increase, while *Festuca ovina*, *Nardus stricta*, *Deschampsia flexuosa* and *Vaccinium myrtillus* are greatly reduced, the last two almost to vanishing point. *Trifolium repens*, although not recorded in the analysis, is present on the flushed area and has certainly spread in the last year or two. This species is quite absent from the unflushed area.

#### DISCUSSION OF RESULTS

*Soil.* The outstanding feature in the results is the remarkable change in acidity relationships brought about by flushing. In every case flushing has raised the *pH* and exchangeable calcium and lowered the amount of calcium required to bring the soil to a definite *pH*. The differences between the flushed and unflushed soils are in some cases very great, the increase in *pH* due to flushing amounting to well over 1 unit in several cases, and the amount of exchangeable calcium being increased several-fold.

It is obvious from the figures that the effect of flushing has been to bring about a great improvement in the lime status of the soils, and in most of the areas the soils after treatment could be regarded as satisfactory for pasture growth as far as lime is concerned. The actual improvement in the herbage, however, will depend on the presence of certain nutrients, especially phosphate and potash.

The tests applied for readily soluble phosphate and potash indicate that, so far as potash is concerned, the soils compare favourably with cultivated soils in a good state of fertility. In phosphate, however, except in samples 1 and 2, there appears to be a very marked deficiency, judged by the standard of good cultivated soils. The amount of improvement of the pastures from flushing has therefore probably been limited greatly by the phosphate deficiency.

*Vegetation.* Flushing generally results in an increase in the total number of green shoots of all species considered collectively (cf. Table IV), which may be taken as indicative of an increase in vigour of growth of the plants, and is accompanied by a reduction in the amount of moss present in the turf. The different species, however, are not all affected in the same way, certain species being encouraged by the treatment while others tend to be suppressed. Thus *Agrostis* spp., *Festuca rubra*, *Holcus lanatus*, *Trifolium repens*, and in the one case where it occurred, *Poa trivialis*, all contribute more abundantly to the herbage of the flushed than to that of the unflushed areas, while *Festuca ovina*, *Deschampsia flexuosa*, *Galium saxatile* and *Vaccinium myrtillus* are reduced. *Anthoxanthum odoratum* behaves somewhat irregularly, but on the very acid and markedly peaty soil of area 6 it is distinctly favoured by flushing. *Nardus stricta*, where present in quantity, suffers a reduction as a result of the treatment. Other species are present in too small quantity to allow of very definite conclusions in regard to their behaviour.

Table IV. *The figures show the percentage composition of each area in numbers of shoots of constituent species. Vegetation of flushed and unflushed areas, Boghall Glen*

Area ...	1		2		3		4		5		6	
	U.	F.	U.	F.	U.	F.	U.	F.	U.	F.	U.	F.
Flushed (F.) or unflushed (U.)...	%	%	%	%	%	%	%	%	%	%	%	%
<i>Agrostis</i> spp.	26.3	71.9	37.2	38.6	40.2	57.5	24.9	58.0	29.1	43.2	10.0	30.7
<i>Festuca ovina</i>	50.8	14.7	29.0	13.4	35.5	14.6	41.0	28.4	49.2	13.0	22.3	3.5
<i>F. rubra</i>	—	11.5	11.2	20.4	1.5	17.5	1.6	6.9	9.3	31.3	—	—
<i>Anthoxanthum odoratum</i>	0.9	—	—	—	4.4	2.4	1.1	2.1	1.2	2.1	0.5	5.7
<i>Holcus lanatus</i>	—	—	Trace	4.1	0.1	0.9	—	0.2	1.2	2.4	0.8	28.2
<i>Poa pratensis</i>	0.1	0.4	4.1	3.1	—	0.5	—	0.9	0.5	1.0	—	1.0
<i>P. trivialis</i>	—	—	—	6.4	—	—	—	—	—	—	—	—
<i>Nardus stricta</i>	—	—	—	—	4.0	3.4	1.8	0.5	4.8	2.9	44.0	20.8
<i>Deschampsia flexuosa</i>	—	—	—	—	Trace	—	6.4	0.6	—	—	9.2	—
Other grasses	—	Trace	3.2	0.8	0.4	Trace	0.1	Trace	1.1	0.2	0.2	8.6
<i>Trifolium repens</i>	Trace	—	6.8	9.0	0.1	1.5	—	—	0.3	2.7	—	—
<i>Galium saxatile</i>	16.2	0.5	2.6	0.3	10.0	0.6	9.6	1.1	0.4	0.1	0.1	—
<i>Luzula campestris</i>	2.5	—	0.3	0.1	2.6	0.7	1.0	0.4	0.5	1.1	0.2	0.2
<i>Vaccinium myrtillus</i>	—	—	—	—	0.4	—	11.7	0.5	—	—	12.4	—
Other species	3.2	1.0	5.6	3.8	0.8	0.4	0.8	0.4	2.5	0.2	0.3	1.3
Total shoots (all species)	4144	5867	6015	8990	5769	8209	4978	8353	2597	3580	3854	3700

In considering the reactions of the various individual species to treatment by irrigation it is necessary to bear in mind that the plants are growing, not in pure stands but in mixed communities. This is important, because the question of interspecific competition is involved. Thus, for example, *Festuca ovina* generally shows a reduction in its contribution to the sward as a result of flushing, but in one case (area 4) the number of shoots of this species was actually increased, and the apparent reduction is due to the fact that the increase was proportionally less than the increase in the total number of shoots of all species. Even where the number of shoots of a species is reduced it does not follow that the treatment has had a directly adverse effect on the species in question. It may equally well be the case that the treatment has reacted favourably upon it but even more favourably upon its competitors, and that the increased competition which the species has had to meet has more than balanced the beneficial effect of flushing. Experiments conducted upon a mixed herbage do not permit of conclusions as to the behaviour of individual species growing alone, and this may account in part for the irregularity in behaviour of certain species. If the question is considered, however, from the point of view of the community as a whole the results are fairly consistent throughout, certain species being regularly favoured by the treatment while others are equally regularly reduced. In view of the marked alterations in the soil which follow upon flushing it seems reasonable to conclude that the alteration in balance of the vegetation is dependent upon the change in soil conditions.

The last statement, however, requires some qualification. It has frequently been observed that sheep show a marked preference for areas which have been subjected to irrigation, and the increased grazing and treading which accompany this must presumably exercise some effect upon the herbage. It might be suggested that the changes which follow upon flushing are to be attributed to biotic rather than to edaphic factors, although it may be mentioned that close cutting of the herbage without any treatment of the soil has not upset the balance of the vegetation in anything like the same way as has been done by flushing.

This question was experimentally investigated in one case (area 6) where part of the area was enclosed by a wire fence, grazing and treading being thus completely excluded over a period of some years. Samples from the flushed and unflushed vegetation within this fence were analysed botanically and the results for the more important species are given in Table V, together with the corresponding figures for the section outside the enclosure which was grazed in the usual way.

Inspection of these figures does not suggest that biotic influences are the controlling factor in effecting the changes in the vegetation which occur after flushing. There is manifestly a closer resemblance between the herbage of the grazed and ungrazed sections of the flushed ground than between the flushed

and unflushed ground. The effect of protection from grazing on unflushed ground has been to upset the balance between *Nardus*, *Deschampsia* and *Vaccinium*, increasing the last two at the expense of the first, but *Anthoxanthum*, *Festuca ovina* and *Holcus* have not been affected at all and *Agrostis* only to a minor extent. Irrigation, on the other hand, has effected a marked increase in *Holcus*, *Anthoxanthum* and *Agrostis*, both in the presence and in the absence of grazing, along with a decided reduction in *Festuca ovina*, *Deschampsia* and *Vaccinium*. *Nardus* is the only species which has behaved in an irregular way, and it is noteworthy that, on unflushed ground, this species is reduced, and not increased, by being protected from grazing, i.e. the effect of grazing is directly opposite to that of flushing.

Table V. *The effect of protection from grazing on the botanical composition of flushed and unflushed pasture*

	Unflushed		Flushed	
	Ungrazed %	Grazed %	Ungrazed %	Grazed %
<i>Nardus stricta</i>	20.0	44.0	23.1	20.5
<i>Festuca ovina</i>	21.6	22.3	12.9	3.5
<i>F. rubra</i>	—	—	3.9	—
<i>Agrostis</i> spp.	3.7	10.0	20.5	30.4
<i>Deschampsia flexuosa</i>	28.6	9.2	4.3	—
<i>Anthoxanthum odoratum</i>	0.2	0.5	12.3	5.6
<i>Holcus lanatus</i>	0.2	0.8	19.6	27.9
<i>Poa pratensis</i>	—	—	0.4	1.0
<i>Vaccinium myrtillus</i>	25.4	12.4	1.2	—

It seems legitimate, therefore, to conclude that biotic factors, while they may exert a modifying influence on the herbage, are not primarily responsible for the characteristic changes in the herbage which follow upon flushing, and it is necessary to seek for the explanation of these changes in the alteration in soil conditions which flushing induces.

As the outstanding change in soil conditions induced by flushing is a marked improvement in the lime status of the soil, it may be of interest to compare the changes in the vegetation in the present series of experiments with changes recorded elsewhere as a result of the application of lime.

Brenchley (1924) has discussed the results of liming on the herbage of the Park meadow hay plots at Rothamsted. Summarising the Rothamsted results for the species occurring in the present experiments, we find marked differences in the behaviour of individual species in the two cases. Thus *Agrostis* at Rothamsted was generally considerably reduced by liming, *Anthoxanthum* was generally reduced, *Festuca ovina* varied in its response and *Holcus lanatus*, where the acidity was high, also suffered reduction. It must be remembered, however, that the conditions under which the Rothamsted experiments have been carried out differ very widely from the conditions obtaining in the present experiments. Apart from the difference in geographical position and thus in climatic conditions, the Rothamsted plots have been cut for hay twice every



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year for an extended period. The whole position as regards competitive interaction between different species must thus have been radically different in the two cases, and it is perhaps not surprising that the results have been entirely different also.

More germane to the present case are two series of investigations on grazed pastures in Yorkshire reported on by Lynn and Lynn (1924), and Hunter and Millard (1927). Lynn and Lynn report that on acid pastures dominated by *Nardus stricta*, the application of lime resulted in a reduction of *Nardus*, *Galium saxatile* and *Potentilla erecta*, and increase of *Festuca ovina*, *Agrostis* spp., *Trifolium repens*, etc. On acid pastures dominated by *Agrostis* spp. liming effected an increase in *Trifolium repens* and sometimes in *Festuca ovina*, while the proportion of *Agrostis* spp. was sometimes reduced. These results resemble generally those recorded in the present paper with some difference, notably the increase in *Festuca ovina* resulting from liming. The result of flushing has generally been to reduce this species in our experiments.

Hunter and Millard found that applications of lime to certain acid pastures resulted in a marked spread of *Trifolium repens*. There was usually also an increase in fine-leaved Fescues (the different species not being distinguished) and frequently *Agrostis* also showed an increase. These results again are somewhat similar to those of flushing, with the exception of the differing behaviour of *Festuca ovina*. *Trifolium repens*, while generally favoured by flushing, has not shown the same marked response as in the case of the liming experiments. It must be remembered, however, that in the present case the soils are extremely deficient in readily soluble phosphate and this may account for the difference.

In general, there appears to be a sufficiently close resemblance between the vegetation changes brought about by flushing and those effected by liming to support the view that the change in acidity relationships and lime status of the soil is one of the important factors responsible, directly or indirectly, for the changes in vegetation which follow upon flushing.

It is, of course, possible and indeed probable that other factors are also involved. The aeration of the soil brought about by flushing has been emphasised by Smith and Crampton (1914) as a possibly important factor, while the effect of the water itself upon moisture relationships in the soil may have a considerable influence. It has not, however, been possible in the course of the present investigation to examine these points.

### SUMMARY

1. An account is given of experiments on flushing or artificial irrigation of hill pastures with spring water; the previous work on the subject is briefly reviewed.

2. The work was carried out on several soil types with water from a number of different springs, some from basic and others from acid rocks. Descriptions

and chemical data relating to the soils, and chemical analyses and conductivity measurements of water samples are given.

3. Irrigation has had the effect, in certain cases very marked, of raising the pH of the soil, increasing the exchangeable calcium, and reducing the amount of calcium required to bring the pH of the soil to a definite figure.

4. *Agrostis* spp., *Festuca rubra*, *Holcus lanatus*, *Trifolium repens* and *Poa trivialis* have been encouraged by the treatment. *Festuca ovina*, *Deschampsia flexuosa*, *Galium saxatile* and *Vaccinium myrtillus* have been reduced. *Nardus stricta*, where abundant, has also suffered reduction.

5. It is considered that the marked changes in reaction and content of calcium brought about in the soil through flushing have played an important part in modifying the vegetation, increasing its amount and rendering it more palatable to stock. The low content of phosphoric acid in all the areas studied except one has probably restricted the amount of improvement in the pasture.

6. Flushing certain soils with suitable water can bring about the same result as an application of lime, and attention is drawn to the possibility of a more extensive use of flushing as a method of improving hill pastures.

#### REFERENCES

- Brenchley, W. E. *The Manuring of Grassland for Hay*, London, 1924.
- Crampton, C. B. *The Vegetation of Caithness considered in relation to the Geology*, 1911.
- Farrow, E. P. *Plant Life on East Anglian Heaths*, Cambridge, 1925.
- Heddle, R. G. and Ogg, W. G. "Experiments in the improvement of hill pasture." *Scot. J. Agric.* **16**, 1933.
- Hunter, R. E. and Millard, W. A. "The improvement of poor pasture in Yorkshire." *Univ. Leeds Bull.* No. 150, 1927.
- Kirsanov, A. T. In *Bull. Leningrad Dept. Inst. Fert. and Agro. Soil Sci.* No. 38, 1932.
- Lynn, J. C. and Lynn, D. A. "Observations on the improvement of poor pasture in the West Riding of Yorkshire." *Ann. App. Biol.* **11**, 1924.
- Report 2nd Internat. Committee for Soil Research, **2**, 1930.
- Robertson, J. *General View of the Agriculture in the County of Perth*, 1799.
- Robie, D. "On English water meadows and how far they are applicable to Scotland." *Trans. Highland and Agric. Soc. Scotland*, Ser. 4, **8**, 1876.
- Robinson, D. H. "The percentage frequency method", in "Methods of Pasture analysis," *Agric. Progr.* **10**, 1933.
- Schollenberger, C. J. and Dreiselbis, F. R. *Soil Sci.* **30**, 1930.
- Singers, W. "General observations on the practice and principles of irrigation." *Trans. Highland and Agric. Soc. Scotland*, Ser. 1, **3**, 1807.
- Smith, A. M. and Coull, R. "The estimation of the buffer capacity of acid soils." *Soil. Res.* **3**, 1932.
- Smith, J. "On the advantages of watering pasture and meadow grounds in the Highlands." *Trans. Highland and Agric. Soc. Scotland*, Ser. 1, **1**, 1799.
- Smith, W. G. "The distribution of *Nardus stricta* in relation to peat." *This JOURNAL*, **6**, 1918*a*.
- Smith, W. G. "The improvement of hill pasture." *Scot. J. Agric.* **1**, 1918*b*.
- Smith, W. G. and Crampton, C. B. "Grassland in Britain." *J. Agric. Sci.* **6**, 1914.

# OVER-DISPERSION IN GRASSLAND COMMUNITIES AND THE USE OF STATISTICAL METHODS IN PLANT ECOLOGY

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(*With six Graphs in the Text*)

ASSUMPTIONS are frequently made as to the mode of distribution of the individuals of plant species in natural vegetation, but there is actually very little exact information on the point. In a paper dealing with "The structure of prairie vegetation", T. L. Steiger (1930) published tables which give the number of individuals of each species observed within 80 m. quadrats. Forty of these quadrats were placed in vegetation described as "high prairie", dominated by *Andropogon furcatus*, and the other forty in "low prairie", with several grasses co-dominant. These data are valuable as a basis for obtaining exact information as to the mode of distribution of the species recorded, and they have been consequently analysed statistically for that purpose.

The units counted by Steiger are described as "individuals", but, as Romell (1930) has pointed out, this term must be taken to mean "rooted shoots", since it is impossible to use any other satisfactory criterion of individuality.

The quadrats were all 1 sq. m. in area. "The forty quadrats on low prairie were selected at regular intervals along four parallel lines. A similar number were selected on the upland with the express purpose of including various portions of tract upon which the vegetation was much more diversified." The two sets of quadrats can be supposed, therefore, to represent more or less random samples of two "communities" recognised by Steiger.

## RELATIVE VARIANCE

The simplest assumption, and the one most frequently made, concerning the distribution of the individuals of a plant species, is that it is random, i.e. that the chance that an individual shall occur in a given spot is the same for all spots, and is therefore independent of the position of other individuals of the species. It is then easy to show that the chances that 0, 1, 2, 3, ... individuals shall occur in a sample area large enough to contain very many individuals, are given by the terms of the Poisson series:

$$e^{-m} (1, m, \frac{m^2}{2!}, \frac{m^3}{3!}, \dots),$$

where  $m$  = the average number of individuals in areas equal to the sample area, and  $n! = n \cdot n - 1 \cdot n - 2 \dots 1$ . If observations are made on a large number of similar sample areas located at random, the terms of the Poisson series give the expected fractions of the total number in which 0, 1, 2, 3, ... individuals will be found. With a finite number of sample areas the observed fractions will not exactly equal these calculated fractions, but a test can be applied, the  $\chi^2$  test, to find whether the discrepancies are to be taken as indicating a real divergence from the Poisson distribution or merely as sampling errors.

A convenient property of the Poisson series is that the variance ( $V$ ) is equal to the mean ( $m$ ) for all values of  $m$ , so that the relative variance,  $V/m$ , is

Table I

Species		$m$	$V/m$	$F$
<i>Sisyrinchium campestre</i>	*L.P.	0.250	†0.97	0.225
<i>Eragrostis pectinacea</i>	L.P.	0.350	†0.96	0.300
<i>Psoralea floribunda</i>	L.P.	0.375	†1.49	0.175
<i>Echinacea pallida</i>	L.P.	0.375	1.74	0.225
<i>Polygala verticillata</i>	L.P.	0.525	3.42	0.200
<i>Viola pedatifida</i>	L.P.	0.575	†1.15	0.400
<i>Meibomia illinoensis</i>	L.P.	0.625	1.70	0.375
<i>Drymocallis agrimonioides</i>	L.P.	0.675	10.59	0.075
<i>Eragrostis pectinacea</i>	*H.P.	0.775	4.20	0.325
<i>Petalostemon candidum</i>	L.P.	0.800	1.68	0.425
<i>Elymus canadensis</i>	H.P.	1.275	15.64	0.175
<i>Aster multiflorus</i>	H.P.	1.350	4.35	0.400
<i>Cathartolinum sulcatum</i>	H.P.	1.375	4.35	0.550
<i>Erigeron ramosus</i>	L.P.	1.725	1.46	0.700
<i>Cathartolinum sulcatum</i>	L.P.	1.825	2.83	0.625
<i>Helianthus scaberrimus</i>	H.P.	1.850	5.56	0.500
<i>Erigeron ramosus</i>	H.P.	2.175	3.06	0.625
<i>Psoralea argophylla</i>	L.P.	2.375	6.34	0.475
<i>Aster multiflorus</i>	L.P.	2.525	6.66	0.500
<i>Elymus canadensis</i>	L.P.	2.625	14.47	0.375
<i>Psoralea floribunda</i>	H.P.	2.675	2.65	0.850
<i>Solidago glaberrima</i>	H.P.	3.225	19.52	0.475
<i>Koeleria cristata</i>	L.P.	3.300	3.11	0.675
<i>Amorpha canescens</i>	L.P.	4.700	6.77	0.850
<i>Carex pennsylvanica</i>	H.P.	5.025	6.67	0.825
<i>Stipa spartea</i>	L.P.	5.400	4.96	0.825
<i>Antennaria campestris</i>	H.P.	6.025	22.30	0.500
<i>Solidago glaberrima</i>	L.P.	6.450	10.50	0.700
<i>Helianthus scaberrimus</i>	L.P.	6.625	12.48	0.825
<i>Carex meadii</i>	L.P.	6.975	7.18	0.825
<i>Amorpha canescens</i>	H.P.	9.875	5.30	1.000
<i>Koeleria cristata</i>	H.P.	10.725	4.73	0.950
<i>Sporobolus heterolepis</i>	H.P.	12.075	11.10	0.775
<i>Stipa spartea</i>	H.P.	12.775	20.66	0.825
<i>Antennaria campestris</i>	L.P.	14.575	10.24	0.775
<i>Carex meadii</i>	H.P.	16.175	17.28	0.950
<i>Andropogon scoparius</i>	L.P.	22.275	20.91	0.950
<i>Bouteloua curtipendula</i>	L.P.	24.500	31.06	0.750
<i>Poa pratensis</i>	H.P.	25.325	37.54	1.000
<i>Andropogon scoparius</i>	H.P.	28.375	17.70	1.000
<i>Bouteloua curtipendula</i>	H.P.	38.400	17.74	1.000
<i>Andropogon furcatus</i>	H.P.	38.925	23.33	0.975
<i>Poa pratensis</i>	L.P.	86.400	9.60	0.975
<i>Andropogon furcatus</i>	L.P.	111.525	14.12	1.000

$m$  = mean density.  $V/m$  = relative variance.  $F$  = frequency index.

\* L.P. = low prairie; H.P. = high prairie.

† Odds of less than 19 : 1 against Poisson distribution as determined by  $\chi^2$  test.

always unity. If in a set of counts of numbers of individuals per sample area the relative variance is greater than unity, this indicates that the dispersion is greater than would be expected on the assumption of random (Poisson) distribution. Alternatively, if the relative variance is less than unity, the dispersion is less than would be expected. The first condition, over-dispersion, implies that individuals are scattered less evenly, and the second, under-dispersion, that they are scattered more evenly than would be expected.<sup>1</sup>

Table I gives the estimates of relative variance for all those species about which the data gave adequate information. The estimate of relative variance was calculated as

$$\frac{\sum_1^n \frac{(x-m)^2}{(n-1)m}}$$

i.e. the square of the estimated standard deviation divided by the mean. It is at once seen that with only two exceptions  $V/m$  is always greater than unity, and reaches the very high value of 37.54 for *Poa pratensis* in high prairie. It is also evident that  $V/m$  tends to increase with  $m$ . This is shown in Fig. 1, where  $V/m$  is plotted against  $m$  for all the species taken. The points are widely scattered but the curve of best fit through grouped mean values rises steadily to a point where a relative variance 24.08 corresponds with a mean of 32.75. Thereafter the curve seems to fall, a feature that must be considered later.

We may conclude, then, that a great majority of the species in these two communities are certainly not distributed in the simple Poisson mode. The divergence is least in species with a low mean density—i.e. in the rare species—and increases rapidly as the density increases. The divergence is in the direction of over-dispersion, as is readily seen by comparing the expected fractions of the total number of quadrats in which 0, 1, 2, ... individuals are found, with the corresponding observed values. Figs. 2 and 3 show this relation graphically for a few species. In Fig. 2 four species have been selected in which the mean density is low. The observed values are quite close to expectation in *Sisyrinchium campestre* ( $m=0.25$ ;  $V/m=0.97$ ), so close in fact that the two curves cannot be separated in the graph. In *Viola pedatifida* ( $m=0.575$ ;  $V/m=1.15$ ) and *Echinacea pallida* ( $m=0.375$ ;  $V/m=1.74$ ) the characteristic type of divergence is beginning to appear, with a slight excess in classes 0, 2, 3 and 4, and a corresponding deficit in the 1 class. In *Petalostemon candidum* ( $m=0.8$ ;  $V/m=1.68$ ) the excess in the 0 class is more marked. The last two species shown in Fig. 2 are representative of the majority in the excess over expectation in extreme classes and the deficit in central classes.

The  $\chi^2$  test may be applied to show whether the deviations from Poisson distribution should be regarded as real. The data must be grouped for this purpose so that no expected number is very small. The result of applying the test to the grouped data is given in Table II, which shows that the hypothesis

<sup>1</sup> These terms are susceptible of two opposite interpretations, but it has been customary to use under- and over- (or hypo- and hyper-) as referring to the relation of the measure of dispersion to its value for a Poisson distribution.

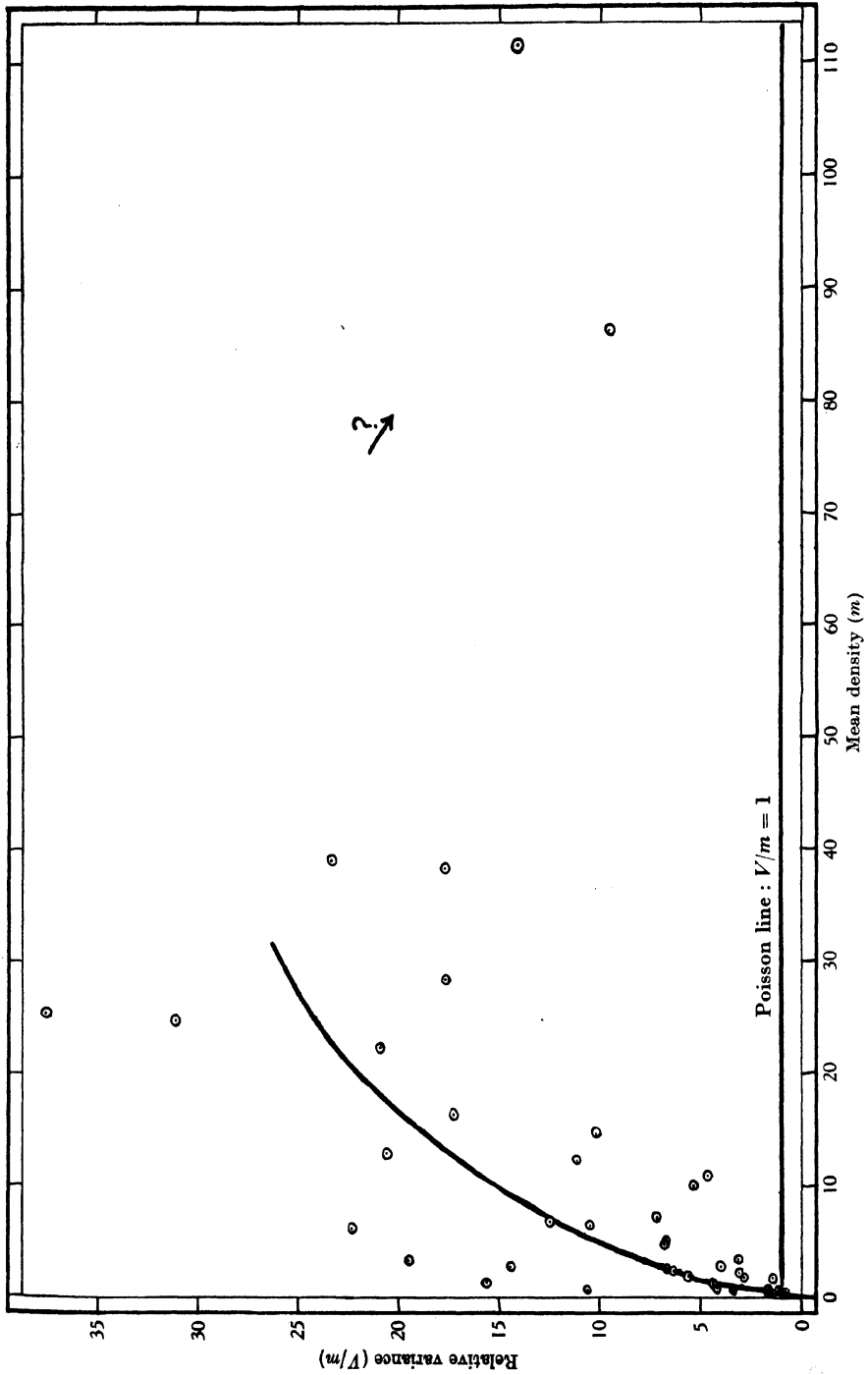


FIG. 1. Graph showing relation of mean density ( $m$ ) to relative variance ( $V/m$ ) for 44 species. The line parallel to the X-axis at  $V/m = 1$  shows the expected relation on the assumption of random distribution of individuals.

of Poisson distribution is not disproved for *Sisyrhynchium campestre* or *Viola pedatifida*, but for *Echinacea pallida* and *Petalostemon candidum* the odds are about 25 to 1 against it. For the species of Fig. 3, and therefore for the great majority of species, the odds against the truth of the hypothesis are so great that it may be ruled out. There are in all four species out of the forty-four studied for which the odds against the hypothesis are less than 19 to 1 (see

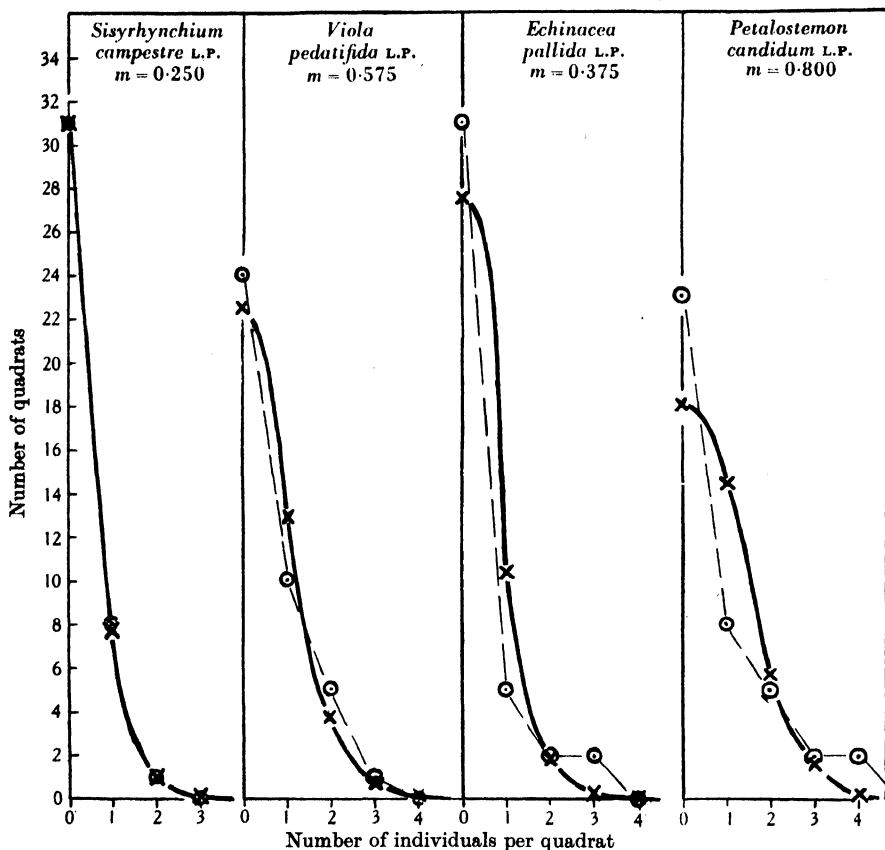


FIG. 2. Frequency curves of numbers of individuals per quadrats for 4 rare species. The broken line connects observed frequencies, and the continuous line passes through calculated frequencies for the Poisson series with corresponding means. L.P. = low prairie.

Table I). The distribution of the individuals of most species is much more patchy than the hypothesis allows. Too many quadrats contain no individuals, or a small number, and too many contain a large number of individuals. In other words the individuals are aggregated in patches so that relatively few quadrats contain an average number, and this patchiness becomes more marked as the average density increases. The relation with density is not, however, a close one, so that it would be impossible to estimate the mode of distribution with any useful accuracy merely from a knowledge of the mean density.

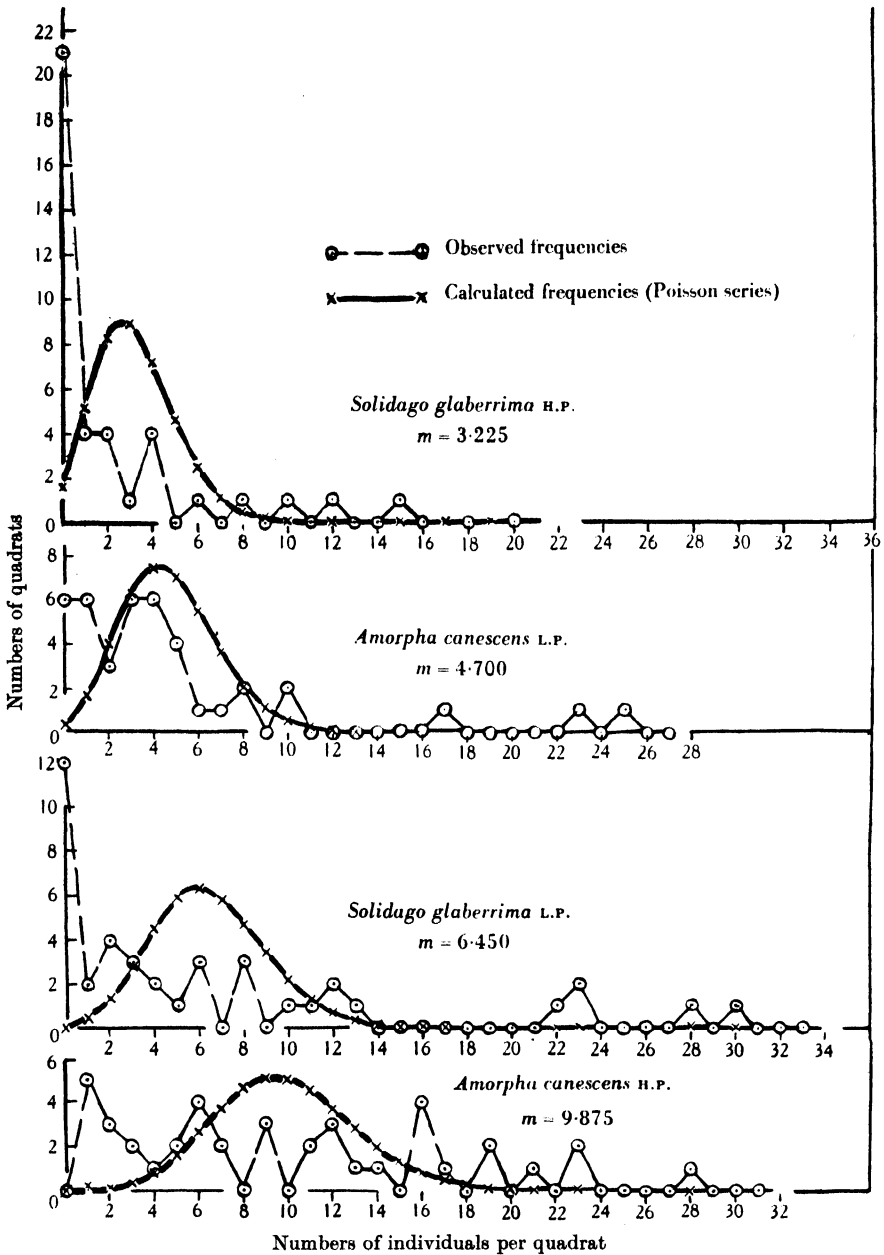


FIG. 3. Frequency curves of numbers of individuals per quadrat for *Solidago glaberrima* and *Amorpha canescens*, each in high prairie (H.P.) and low prairie (L.P.).



Table II

<i>Sisyrinchium campestre</i> L.P.			<i>Viola pedatifida</i> L.P.			<i>Echinacea pallida</i> L.P.			<i>Petalostemon candidum</i> L.P.			
Observed	Calculated		Observed	Calculated		Observed	Calculated		Observed	Calculated		
0	31	31.19	24	22.53		31	27.52		23	17.97		0
1	8	7.22	10	12.91		5	10.27		8	14.38		1
2	1	0.99	5	3.72		2	1.94		5	5.75		2
3	—	—	1	0.72		2	0.25	2.21	2	1.53		3
4	—	0.01	—	0.10	4.56	—	0.02	—	2	0.31	7.65	4
5	—	—	—	0.01	—	—	—	—	—	0.05	—	5
6	—	—	—	—	—	—	—	—	—	0.01	—	6
$\chi^2=0.02$ $p=.85$			$\chi^2=1.21$ $p=.27$			$\chi^2=4.59$ $p=.04$			$\chi^2=4.48$ $p=.04$			
<i>Aster multiflorus</i> L.P.			<i>Aster multiflorus</i> H.P.			<i>Solidago glaberrima</i> L.P.			<i>Solidago glaberrima</i> H.P.			
Observed	Calculated		Observed	Calculated		Observed	Calculated		Observed	Calculated		
0	20	3.12	24	10.38		12	0.06		21	1.59		0
1	6	7.95	5	13.99		2	0.41		4	5.13	6.72	1
2	2	10.15	4	9.44	9.44	4	1.32	9.18	4	8.27	8.27	2
3	1	8.63	1	4.25		3	2.83		1	8.89	8.89	3
4	2	5.51	1	1.44		2	4.56		4	7.17	7.17	4
5	2	2.81	3	0.39		1	5.88	5.88	—	4.62		5
6	1	1.20	—	0.09		3	6.32	6.32	1	2.49		6
7	1	0.44	—	0.02		—	5.82		—	1.15		7
8	2	0.14	—	—		3	4.70	10.52	1	0.46		8
9	—	0.04	1	—		—	3.37		—	0.18		9
10	1	0.01	1	—		1	2.17		1	0.05		10
11	—	—	—	—		1	1.27		—	0.01		11
12	—	—	—	—		2	0.68		1	—		12
13	1	—	—	—		3	0.34		—	—		13
14	—	—	—	—		—	0.16		—	—		14
15	—	—	—	—		—	0.07		1	—		15
16	—	—	—	—	6.19	—	0.03		—	—		16
17	—	—	—	—	—	—	0.01		—	—	8.96	17
18	1	—	—	—	—	—	—	8.10	—	—	—	18
19	—	—	—	—	—	—	—	—	—	—	—	19
20	—	—	—	—	—	—	—	—	—	—	—	20
21	—	—	—	—	—	—	—	—	—	—	—	21
22	—	—	—	—	—	1	—		—	—	—	22
23	—	—	—	—	—	1	—		—	—	—	23
24	—	—	—	—	—	—	—		—	—	—	24
25	—	—	—	—	—	—	—		—	—	—	25
26	—	—	—	—	—	—	—		—	—	—	26
27	—	—	—	—	—	—	—		—	—	—	27
28	—	—	—	—	—	—	—		—	—	—	28
29	—	—	—	—	—	—	—		—	—	—	29
30	—	—	—	—	—	—	—		—	—	—	30
31	—	—	—	—	—	—	—		—	—	—	31
32	—	—	—	—	—	—	—		—	—	—	32
33	—	—	—	—	—	—	—		—	—	—	33
34	—	—	—	—	—	—	—		—	—	—	34
35	—	—	—	—	—	—	—		—	—	—	35
36	—	—	—	—	—	—	—		—	—	—	36
37	—	—	—	—	—	—	—		—	—	—	37
38	—	—	—	—	—	—	—		—	—	—	38
39	—	—	—	—	—	—	—		—	—	—	39
40	—	—	—	—	—	—	—		—	—	—	40
41	—	—	—	—	—	—	—		—	—	—	41
42	—	—	—	—	—	—	—		—	—	—	42
43	—	—	—	—	—	—	—		—	—	—	43
44	—	—	—	—	—	—	—		—	—	—	44
45	—	—	—	—	—	—	—		—	—	—	45
46	—	—	—	—	—	—	—		—	—	—	46
47	—	—	—	—	—	—	—		—	—	—	47
$\chi^2=33.50$ $p<10^{-6}$			$\chi^2=26.79$ $p=c. 10^{-6}$			$\chi^2=33.02$ $p<10^{-6}$			$\chi^2=61.35$ $p<10^{-6}$			

## RAUNKIAER FREQUENCY AND DENSITY

Jaccard (1908) and Raunkiaer (1909) devised and used extensively a technique for quantitative observation in vegetation, consisting in recording merely the presence or absence of a species in each of a large number of sample areas within the piece of vegetation under investigation. This method obviated the necessity for actually counting individuals, the "frequency", "frequency index" or "Raunkiaer frequency" of a species being the fraction or percentage

of sample areas in which the species was present, whether as one individual or many. It was soon realised that this figure must vary with the size of sample, and various standard sizes and shapes of sample have been suggested for the determination of frequency indexes. It was realised, too, that even with a fixed size of sample the relation of frequency index to density is not linear, but it was believed by many that the relation could be calculated from the assumption that individuals of a species are distributed at random, or could be determined empirically and used in subsequent work.

Steiger's data provide an opportunity for investigating this problem in grassland. In Fig. 4 frequency index is plotted against density for all species for which adequate information is available. The data from which the graph is

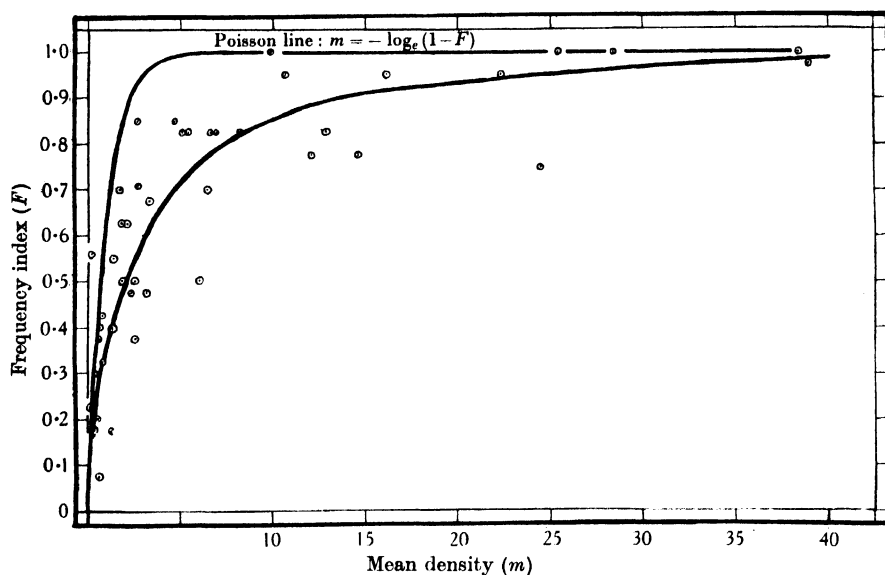


FIG. 4. Relation between frequency index ( $F$ ) and mean density ( $m$ ) for 44 species. The upper line shows the calculated relation for random distribution of individuals.

constructed are shown in Table I. The points are very much scattered, but the curve through grouped mean values rises rapidly at first, then progressively less rapidly as a frequency index of 1 is approached.

It is easy to calculate an "expected" curve on the assumption of random distribution. For if  $m$  is the mean number of individuals per quadrat, the fraction containing 0 individuals is  $e^{-m}$ , and the fraction containing 1 or more is therefore  $1 - e^{-m}$ . Thus the frequency index is related to density by the equation

$$F = 1 - e^{-m} \quad \text{or} \quad m = -\log_e(1 - F).$$

The curve showing this relation is plotted in Fig. 4 for comparison with the observed curve. It is at once evident that the frequency index rises much less rapidly with density than would be expected. On the theory of random distribution  $F$  should be 0.90 when  $m$  is 2.3, and 0.99 when  $m$  is 4.6. Actually

the average observed values are about 0.60 and 0.71 respectively. This is another expression of the fact already stated that there is usually an excess of quadrats in which a given species is not found at all.

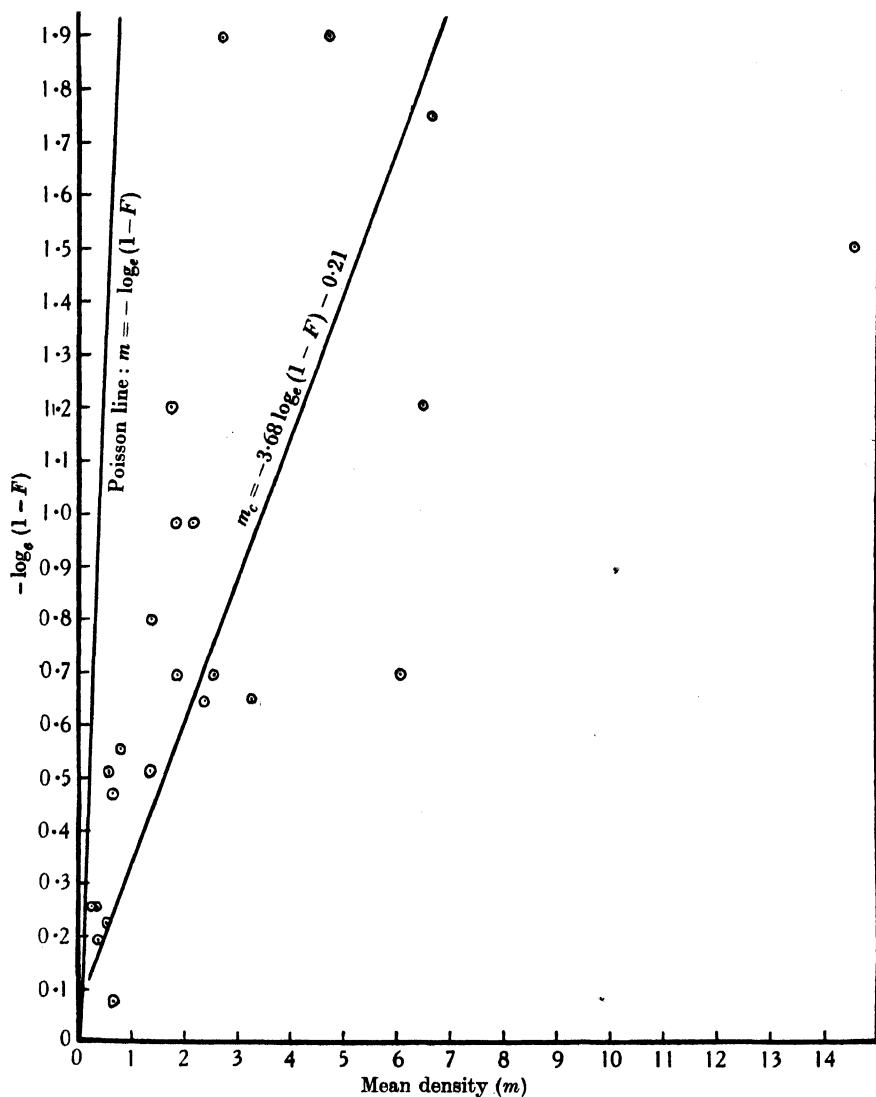


Fig. 5. As Fig. 4 but  $m$  plotted against  $-\log_e(1-F)$  for 23 non-grassy species. The steeper line is that for random distribution of individuals, the less steep that of best fit to the observed points.

Fig. 5 illustrates the divergence from random distribution in curves obtained by plotting mean density against  $-\log_e(1-F)$  for non-grassy species only. The observed points fall about a line whose equation is

$$m_c = -3.68 \log_e(1-F) - 0.21.$$

There is some indication that with higher densities a curved line would give a better fit than the straight line, but it may be said that the relation between density and frequency is logarithmic within the observed range. The slope of the line is, however, much less steep than that of the Poisson relation, also shown in Fig. 5.

That the relation is not that calculated on the assumption of random distribution does not in itself invalidate the Raunkiaer method. A much more serious objection is that different species behave differently. The curves in Figs. 4 and 5 only show average relations: the actual points are widely scattered round them. It would be impossible to estimate the density of a species from its frequency index with any useful accuracy even if one knew the relation represented by these curves. Columns 5 and 6 of Table III (showing the mean densities calculated from the curve of Fig. 5 and their relation to the observed mean densities) illustrate this point sufficiently well. It is possible that a curve constructed from observations on a single species in different areas might be of value for estimating the density of that species in other areas by the frequency index method. But it might well be found that its mode of distribution varied according to the species associated with it, so that in two areas the same frequency index might correspond with quite different densities. That such disturbing changes do occur is well shown in *Erigeron ramosus*, which has mean density 1.73 in low prairie and 2.18 in high prairie, the corresponding frequency indexes being 0.70 and 0.63. The increased dispersion in high prairie has been sufficient to lower the frequency index although the mean density has risen.

Table III

Species		<i>m</i>	<i>F</i>	<i>m<sub>c</sub></i>	<i>m<sub>c</sub>/m</i>
<i>Sisyrinchium campestre</i>	L.P.	0.250	0.225	0.728	2.91
<i>Psoralea floribunda</i>	L.P.	0.375	0.175	0.497	1.33
<i>Echinacea pallida</i>	L.P.	0.375	0.225	0.728	1.94
<i>Polygala verticillata</i>	L.P.	0.525	0.200	0.611	1.16
<i>Viola pedatifida</i>	L.P.	0.575	0.400	1.670	2.90
<i>Meibomia illinoensis</i>	L.P.	0.625	0.375	1.520	2.43
<i>Drymocallis agrimonioides</i>	L.P.	0.675	0.075	0.266	0.39
<i>Petalostemon candidum</i>	L.P.	0.800	0.425	1.825	2.28
<i>Aster multiflorus</i>	H.P.	1.350	0.400	1.670	1.24
<i>Cathartolinum sulcatum</i>	H.P.	1.375	0.550	2.730	1.99
<i>Erigeron ramosus</i>	L.P.	1.725	0.700	4.206	2.44
<i>Cathartolinum sulcatum</i>	L.P.	1.825	0.625	3.400	1.86
<i>Helianthus scaberrimus</i>	H.P.	1.850	0.500	2.340	1.26
<i>Erigeron ramosus</i>	H.P.	2.175	0.625	3.400	1.56
<i>Psoralea argophylla</i>	L.P.	2.375	0.475	2.160	0.91
<i>Aster multiflorus</i>	L.P.	2.525	0.500	2.340	0.93
<i>Psoralea floribunda</i>	H.P.	2.675	0.850	6.771	2.53
<i>Solidago glaberrima</i>	H.P.	3.225	0.475	2.160	0.69
<i>Amorpha canescens</i>	L.P.	4.700	0.850	6.771	1.44
<i>Antennaria campestris</i>	H.P.	6.025	0.500	2.340	0.39
<i>Solidago glaberrima</i>	L.P.	6.450	0.700	4.206	0.65
<i>Helianthus scaberrimus</i>	L.P.	6.625	0.825	6.204	0.94
<i>Antennaria campestris</i>	L.P.	14.575	0.775	5.281	0.36

*m* = observed mean density. *F* = frequency index.

*m<sub>c</sub>* = calculated mean density =  $-3.68 \log_e (1 - F) - 0.21$ .

It can be concluded that the frequency index is of little value as a basis for estimating the density of the constituent species of high and low prairie, since its relation to density varies too widely with the way in which the individuals of these species are distributed.

#### NUMBER OF SPECIES PER QUADRAT

Since the work of Jaccard (1908 *et seq.*), many ecologists have been interested in the relation between the area of a piece of vegetation and the total number of species found in it. Some, like Palmgrèn (1916) and Arrhenius (1920, 1921), have been mainly concerned with determining empirically the nature of the relation; but others, including Romell (1920) and Kylin (1923 and 1926), have endeavoured to deduce the relation from theoretical considerations. The starting point for these theoretical investigations has always been the assumption, with little or no qualification, that individuals of all species are distributed at random.

The data of Steiger do not provide much information on this point, since quadrats of the same size are used throughout. It would be possible, however, though very laborious, to compare the actual numbers of different species occurring in each quadrat with the numbers which would be expected on the assumption of random distribution. To show the nature and extent of the divergence from expectation it is sufficient to consider the occurrences of a small number of species. The four most abundant herbs (excluding grasses and sedges) of high prairie are *Amorpha canescens*, *Antennaria campestris*, *Solidago glaberrima*, and *Psoralea floribunda*, with mean densities of 9.875, 6.025, 3.225 and 2.675 respectively. Using these mean densities it is not difficult to calculate numbers of quadrats in which 0, 1, 2, 3 and 4 of these species should be expected. Table IV gives the observed and expected numbers.

Table IV

No. of species per quadrat	0	1	2	3	4
Calculated nos. of quadrats	0	0	0.1	4.2	35.7
Observed nos. of quadrats	0	3	7	25	5

Thus 36 of the 40 quadrats on high prairie should contain all four of these herbs, but actually they are all found together only in 5 quadrats. The chance of finding only one of the four in any quadrat is, on the hypothesis of random distribution, 1 in 2500, but actually 3 in 40 fall into this class.

Table V shows a similar calculation for the seven most abundant herbs (excluding grasses and sedges) of low prairie, but the calculated numbers are here based on the assumption that all seven have a density of 2.303, which is slightly lower than that of the least abundant of the seven (*Aster multiflorus*, 2.525). The calculated numbers may be regarded as maximum expectations for all classes except the highest, which represents quadrats containing all seven species.

Table V

No. of species per quadrat	Calculated nos. of quadrats	Observed nos. of quadrats
0	0.0000	1
1	0.0003	1
2	0.0068	3
3	0.1021	2
4	0.9185	10
5	4.9601	8
6	14.8803	7
7	19.1319	8
	<u>40.0000</u>	<u>40</u>

The divergences from the calculated numbers are so striking that little comment is necessary. 17 quadrats contain fewer than five of the seven species, against an expectation of 1. In 1 quadrat none of the seven is found, the calculated chance of this happening being 1 in 250,000, and this, it must be remembered, is a maximum chance based on the assumption that all seven have densities slightly below the lowest.

The general character of the divergence could, of course, be predicted from the over-dispersion already revealed. For each of the seven species there are too many quadrats in which it does not occur at all, or occurs as only a few individuals. There are therefore far too many in which fewer than five of the seven occur together, and correspondingly too small a number in which six or seven of them occur together. In general it can be said that the number of different species occurring in a small area of vegetation is much smaller than would be expected from their mean densities on the assumption of random distribution.

#### DISCUSSION

The result of this analysis is to show very conclusively that the individuals of most of the species occurring at all commonly in low and high prairie in Eastern Nebraska are distributed with strong over-dispersion. Only four species, with mean densities ranging from 0.250 to 0.575 individuals per square metre, have a distribution which cannot be distinguished from random by the appropriate statistical test. The remaining forty, including *Echinacea pallida* and *Polygala verticillata* with mean densities in low prairie of only 0.375 and 0.525 respectively, show significant over-dispersion, that is, the odds against their distribution being random are greater than 19 : 1. Over-dispersion was found also in several species of English chalk grassland (1933), and Mr C. J. Dawkins of this Department finds it in the general salt-marsh community. There seems little doubt that it is a widespread phenomenon.

The reason for this strong over-dispersion is not difficult to find. Many perennial species reproduce vegetatively in a way which causes each pioneer plant to be closely surrounded by its offspring. This is true also of reproduction by seed, but less markedly as the dispersal range of the seeds increases. Steiger

states that seeding plays a very small part in the propagation of prairie species, and that only about 4 per cent. are annuals. The perennial grasses and sedges and several of the non-grassy herbs are propagated by rhizomes and it must be supposed that many of the remaining herbs have some means of vegetative reproduction. It would be interesting to relate the degree of over-dispersion to the mode of propagation for all species studied, but Steiger does not give the necessary detailed information.

It has been explained that a consequence of prevalent over-dispersion is that the mean density of a species cannot be estimated, with useful accuracy, from its frequency index. A more striking consequence is that it is impossible to assess the accuracy even of a direct estimate of density, obtained by counting all the individuals of a species within each quadrat. Suppose, for instance, that it was desired to know whether a certain species had the same mean density in two extensive pieces of vegetation. The only practicable procedure would be to make estimates of the two densities by a sampling method, that is, by the use of numbers of quadrats. If the numbers of individuals in the quadrats are distributed in a Poisson series, or if they are distributed normally (i.e. in the well-known symmetrical curve of errors), it is then possible to make a definite statement as to the probability that the observed densities are two estimates of the same real density. But if the numbers of individuals per quadrat are distributed neither in a Poisson series nor normally, or nearly so, no such statement can be made. It has been shown that most of the observed distributions are not Poisson series, and a glance at Fig. 2 shows that they are also far from normal, being markedly skew even when the corresponding Poisson series gives a fairly symmetrical curve, close enough to a normal distribution to be treated as such. Fig. 6 shows that *Antennaria campestris* in low prairie gives a bimodal curve even with a density as high as 14.575 per metre quadrat. The curve for *Bouteloua curtipendula* ( $m = 24.500$ ) is markedly J-shaped, and only in the two species with highest density in low prairie, *Poa pratensis* and *Andropogon furcatus* ( $m = 86.400$  and  $111.525$  respectively), do the curves become fairly symmetrical. For these two it should be possible to assess the accuracy of estimated mean densities on the assumption of normal distribution and to be little in error; but it can be said with confidence that this can only be done, using metre quadrats, for species of very high density. With less abundant species it might be possible to achieve the same end by increasing the size of the quadrat, as already suggested (Clapham, 1933). Romell (1930) believes, in this connection, that most vegetation is like a mosaic in its structure, the units of the mosaic being patches composed of individuals of one or a few species, and that these units are grouped into a more or less regularly recurrent pattern. A consequence of this would be that the type of dispersion found should vary with the size of the quadrat used. Thus quadrats of about the same size as a single patch would show strong over-dispersion of numbers of individuals per quadrat, but with quadrats the size of the whole recurrent pattern there would

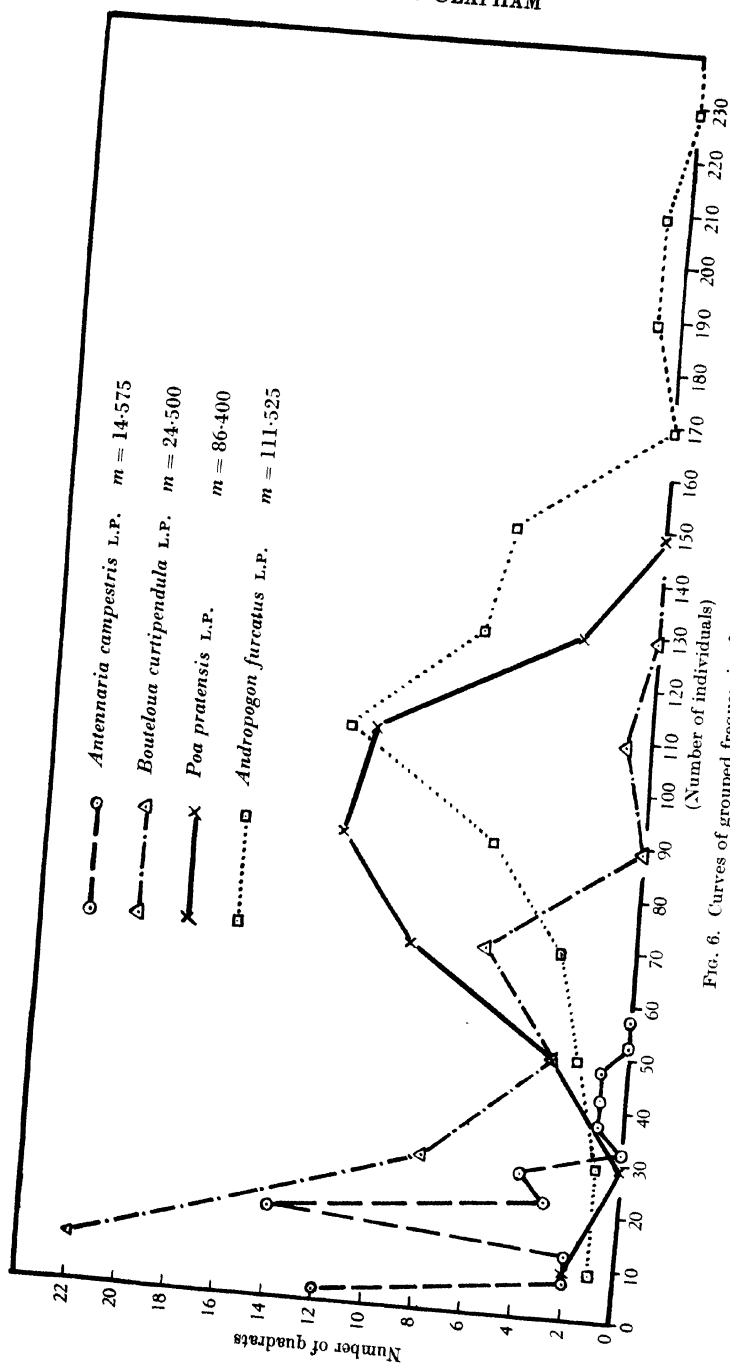


FIG. 6. Curves of grouped frequencies for abundant species.



be under-dispersion. Somewhere in between Romell would expect a quadrat size such that the distribution is "normal", and for this size it would be possible to assess the accuracy of mean densities or to estimate density from frequency indexes. He gives no actual data in support of this, and makes possible exceptions of grassland and meadow communities. In any case the size of quadrat required to give a sensibly normal distribution would have to be determined for each species separately, and the actual labour of counting would be very considerable.

This raises the important question of the value of an estimate of mean density over an extensive area. It may be used for either of two main purposes: as an item in a precise description of a "community" of which the piece of vegetation is regarded as a part or representative, or as a quantitative statement about the vegetation for correlation with quantitative statements about the environment. With regard to the first purpose, it is very dubious whether plant communities can ever be described in precise quantitative statements of floristic, density, luxuriance, etc. On no criterion of isolation are they very sharply defined entities, either in space or time. On what appears to be the most fundamental criterion, that of the nature of the dominant species, a strong physiognomic homogeneity covers much underlying heterogeneity. Close examination often reveals steady or irregular changes in density, mode of dispersion, and luxuriance of the dominants as an area is traversed, and also steady or irregular changes in the floristic composition of the accessory flora, and in the average density, luxuriance, etc. of the individuals of the accessory species. In such a community, then, the average densities of the dominants or of the accessory species may not be sufficiently constant from area to area or from time to time to have any real value as diagnostic criteria. The best defined communities certainly have organisation and stability through shorter or longer periods, but this is of the nature of a dynamic equilibrium. And a real understanding of such communities and of vegetation in general is more likely to be derived from a study of the way in which integration and stability are achieved as a balance of processes than from the most careful description of the average state at a moment. In view, too, of this essentially dynamic interrelation of vegetation and its environment the second main purpose of quantitative ecology, that of correlating precise vegetational and environmental data, cannot be advanced far by methods more truly appropriate to a study of static equilibria. The accurate estimation, supposing it to be possible, of the mean density of a species over a large area and the simultaneous estimation of the average intensities of environmental factors constitutes just such a method.

These remarks are not to be taken as condemnatory of all quantitative work on a statistical scale in vegetational research. On the contrary much can be achieved by the judicious use of a statistical form of precise statement, but the statements must concern relevant phenomena and the labour of arriving

at them must be commensurate with their ecological importance. Such statements are especially appropriate for describing the changes in the space relations of species and individuals as a step towards elucidating the nature of the species mosaic in terms of the interacting forces of invasion pressure, competition, and control by physiographic and biotic agencies. For such purposes the relative variance is a useful index, due attention always being paid to its dependence on quadrat size. Its changes may be traced for each species as succession proceeds. The relating of its early values to the mode of invasion, and of its changes to mode of reproduction and aggregation and ultimately to competition amongst individuals of the species or between them and those of other species, helps to focus attention on these most fundamental characteristics of vegetation, and may lead to an actual assessment of the relative parts played by the various interacting forces. The correlation method suggested by Gleason (1925) and the procedure adopted by Emmett and Ashby (1934) are further examples of a type of statistical work which can be of real value in ecological research quite apart from narrowly sociological aims. The area within which such observations are made depends on the information required, and may be quite small: average values are calculated for these areas, not for extensive communities which may have ill-defined limits.

No extensive data have yet been collected in illustration of these points, but a few results are of interest. On the Dorset coast near Abbotsbury, former arable fields were found in various stages of colonisation by "weeds". The distribution of some of these weeds was studied by the Latin Square method of R. A. Fisher. *Senecio Jacobaea* was the most conspicuous invader, and three 5 × 5 squares were laid down, each with a side of 10 ft.; the small constituent squares being therefore 2 × 2 ft. The squares were laid down in areas where the Ragwort was sparse, denser and very dense, the values of the mean and relative variance being shown in Table VI.

Table VI. *Senecio Jacobaea*

	<i>m</i>	<i>V/m</i>
Sparse	1.67	3.04
Intermediate	3.80	7.95
Dense	12.44	6.09

*m* = mean density per small square. *V/m* = relative variance.

Points of interest are that there is strong over-dispersion throughout, and that the relative variance increases from 3.04 to 7.95 as the density rises from 1.61 to 3.80, but then falls to 6.09 with further increase in density to 12.44. A similar fall at high densities is suggested in Fig. 1, and may be an effect of competition, but it needs closer investigation. In Steiger's data the mode of selection of the quadrats in low prairie for dominance of *Andropogon furcatus* may account for the fall. The initial rise in relative variance is certainly due to aggregation by seeding and vegetative reproduction. The same phenomenon is shown in counts in a small patch of *Blackstonia perfoliata* (annual) where old

flowering shoots of the current year and established seedlings were found together. These were counted separately, and the results are shown in Table VII.

Table VII.  $4 \times 4$  Latin "Square": *Blackstonia perfoliata*

S.W.		N.W.		
2	9	6	1	
2	17	22	3	
0	6	3	0	
6	2	2	0	
0	1	0	0	
0	0	1	0	
3	0	4	2	
1	1	0	1	
2 ft.				

Top figure in each small square: flowering plants of current season:  $m=2.3$ ,  $V/m=2.21$ .

Lower figure in each small square: established seedlings:  $m=3.6$ ,  $V/m=7.70$ .

Here the increase of the relative variance with increased mean density is evidently related to the aggregation of seedlings round a patch of seed parents.

Two other sets of counts made in the same way show the effect of mode of propagation on the relative variance. *Cirsium lanceolatum* and *Pulicaria dysenterica* were both invading over large areas, but the former showed a rather wide scattering of plants, some of them seedlings and some of them older plants with two or more stems, while the latter was in a few dense patches, evidently as a result of rhizome propagation.

	$m$	$V/m$
<i>Cirsium lanceolatum</i>	1.00	0.73
<i>Pulicaria dysenterica</i>	0.81	10.16

Here the mean densities are not very different, but the different modes of propagation are shown in widely divergent relative variances.

These few results concern species in fairly early stages of invasion. As aggregation proceeds over-dispersion becomes increasingly evident, its rate of increase with density depending primarily upon the mode of reproduction. There are suggestions that a maximum dispersion is reached, followed by a decline which is the result of intra- and interspecific competition. With stringent intraspecific competition it is known that under-dispersion may result, individuals being more evenly spaced than if they were distributed at random.

An analysis of these sequences by a quantitative and statistical technique is only justified if relevant information is obtained which could not have been obtained by qualitative observation. It seems likely that such a justification can be claimed for the methods described, especially for the detection of under-dispersion. Over- and under-dispersion both imply that the condition for random distribution is not fulfilled. Over-dispersion means that it is easier for an individual to establish itself close to another individual than further from it, and under-dispersion means that the reverse is true. Most simply, under-dispersion is the result of direct intraspecific competition, as amongst the trees of natural woodland. I am indebted to Prof. R. A. Fisher for the suggestion that it might also arise from the attacks of, say, an insect pest whose migration range is small so that seedlings within a certain distance from a parent plant are at a disadvantage compared with those further away. This might give under-dispersion with individuals separated beyond the range of direct competition. Again, under-dispersion might arise by exclusion of a subordinate species from close proximity to a dominant species which is itself under-dispersed. Yet again it could result from a regular soil fertility pattern, patches suitable for a given species being evenly spaced, as, for instance, in an arctic polygon-soil. Now under-dispersion is not easily evident to mere visual inspection, so that detection of the intra- and interspecific competition and of the hypothetical control by a pest referred to above might be impossible unless a statistical procedure were adopted which gave a sensitive measure of dispersion and of changes in dispersion. Such measures would need to be combined, as occasion suggested, with measures of the co-variance and correlation in space of different species, and should prove valuable tools in ecological research, provided that their users remember always that they are merely tools and that the collection and reduction of numerical data is not a useful end in itself.

Since this paper was accepted for publication two interesting contributions to quantitative ecology by G. E. Blackman (1935) and E. Ashby (1935) have appeared in the *Annals of Botany*. G. E. Blackman finds that five species occurring in certain grassland communities are distributed at random over small areas (0.01–0.02 acre), while others are not. He shows that when distribution of individuals is random or nearly so, the logarithm of percentage absence, using the Raunkiaer technique, is directly proportional to density, and recommends the estimation of percentage absence for the ecological study of botanical changes. It should be noted that in the prairie communities described by Steiger and in a "general salt-marsh community" studied by my pupil Mr C. J. Dawkins only a very few of the rarer species were distributed at random or nearly so. This does not preclude the possibility of a linear relation existing between log percentage absence and density, but if there is such a relation the slope of the line cannot be calculated *a priori*, but must be found by direct observations, and that for each species separately. It seems, moreover, that the mode of distribution of the individuals of many species changes

with density, so that the linear relation can only be an approximate one, for small changes in density; Blackman's observations on *Plantago media* and *Trifolium repens* show a departure from linearity that may be ascribed to this cause.

E. Ashby stresses the essential heterogeneity of vegetation and the primarily physiognomic basis of recognition of plant communities. He confirms the views of Kylin, Romell and others on the logarithmic, not linear, relation between Raunkiaer frequency and density, and exposes again the fundamental unsoundness of the older Scandinavian dogmas regarding "constants". It is fair to point out that du Rietz has for some time ceased to define communities in terms of constants.

Ashby's analysis of the mode of distribution of *Salicornia* on a mud-flat involves the use of a new and valuable technique. It is interesting to find a fairly close approach to random distribution of individuals establishing themselves from seed to form a pure community in as uniform a habitat as the ecologist can hope to find. As far as the evidence goes at present, it seems that only a few of the rarer species of stable communities and some pioneers like *Salicornia* are distributed at random. Ashby's general conclusion, that quantitative methods are of value chiefly in studying the distribution of individual species, is that of the present paper.

#### SUMMARY

1. Data of T. L. Steiger relating to the species found in high and low prairie in Eastern Nebraska are analysed statistically.

2. Statistical units ("individuals") are not, in the great majority of species, distributed at random.

3. The divergence from the expected type of random distribution is conveniently measured by the divergence of the relative variance from unity.

4. Species vary greatly in the extent of their divergence from random distribution.

5. The relative variance is almost always greater than unity, showing over-dispersion of "individuals".

6. The relative variance tends to increase with mean density, but may fall again when the density reaches very high values.

7. Over-dispersion shows itself in an excess of quadrats containing no "individuals" or a large number of "individuals", there being a corresponding deficit in central classes.

8. A consequence of over-dispersion is that the frequency index (Raunkiaer frequency) tends to be much lower than would be expected from the observed density. Its relation to density is roughly logarithmic, but since species vary greatly in their mode of distribution the density of a given species cannot easily be estimated with useful accuracy from its frequency index.

9. A further consequence of over-dispersion is that the number of different species found in a quadrat is on the average much smaller than would be expected from their densities.

10. The accuracy of an estimate of density cannot often be assessed, since the distribution of numbers of individuals per quadrat is neither a Poisson series nor normal.

11. It is suggested that an accurate estimate of the mean density of a species within an extensive community or over a large area does not in itself give very valuable information concerning the community or area.

12. Statistical methods may be used with advantage for investigating the structure of the species mosaic, its changes with time and its relation to the variously interacting forces of invasion pressure, competition and control by physiographic and biotic agencies.

In conclusion I wish to thank Prof. A. G. Tansley for his constant encouragement and advice.

#### REFERENCES

- Arrhenius, O.** "Distribution of the species over the area." *Meddelanden från K. Vetenskapsakademins Nobelinstitut*, **4**, No. 7, 1920.
- Arrhenius, O.** "Species and area." *This JOURN.* **9**, 95-9, 1921.
- Ashby, E.** "The Quantitative Analysis of Vegetation" with an appendix by W. L. Stevens. *Ann. Bot.* **49**, no. 196, pp. 779-802, 1935.
- Blackman, G. E.** "A Study by Statistical Methods of the Distribution of Species in Grassland Associations." *Ann. Bot.* **49**, no. 196, pp. 749-77, 1935.
- Clapham, A. R.** *Proc. Linn. Soc. Lond.* Session 146, Pt. I, 1933.
- Emmett, H. E. D. and Ashby, E.** "Some observations on the relation between the hydrogen-ion concentration of the soil and plant distribution." *Ann. Bot.* **48**, 869-76, 1934.
- Gleason, H. A.** "Species and area." *Ecology*, **6**, 66-74, 1925.
- Jaccard, P.** "Nouvelles recherches sur la distribution florale." *Bull. Soc. Vaudoise Sci. Nat.* 5th Series, **44**, 1908.
- Kylin, H.** "Växtsociologiska Randanmärkningar." *Bot. Notiser*, pp. 161-264, 1923.
- Kylin, H.** "Über Begriffsbildung und Statistik in der Pflanzensoziologie." *Bot. Notiser*, pp. 81-180, 1926.
- Palmgren, A.** "Studier över Lövangsomradena på Åland." No. 3, *Acta Soc. Fauna Flora Fenn.* **42**, 1916.
- Raunkiaer, C.** "Formationsundersøgelse og Formationsstatistik." *Bot. Tids.* **30**, 1909.
- Romell, L. G.** "Sur la Règle de Distribution des Fréquences." *Svensk Bot. Tids.* **14**, 1-20, 1920.
- Romell, L. G.** "Raunkiaer's and similar methods of vegetation analysis and the 'Law of Frequency'." *Ecology*, **11**, 589-96, 1930.
- Steiger, T. L.** "The structure of prairie vegetation." *Ecology*, **11**, 170-217, 1930.

# NATURE AND STRUCTURE OF THE CLIMAX

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(*With Plates VI—XI*)

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## INTRODUCTION

MORE than a century ago when Lewis and Clark set out upon their memorable journey across the continent of North America (1803-6), they were the first to traverse the great climaxes from deciduous woods in the east through the vast expanse of prairie and plain to the majestic coniferous forest of the north-west. At this time the oak-hickory woodland beyond the Appalachians was almost untouched by the ax except in the neighborhood of a few straggling pioneer settlements, and west of the Mississippi hardly an acre of prairie had known the plow. A few years later (1809), Bradbury states that the boundless prairies are covered with the finest verdure imaginable and will become one of the most beautiful countries in the world, while the plains are of such extent and fertility as to maintain an immense number of animals. It appears probable that at this time no other grassland in the world exhibited such myriads of large mammals belonging to but a few species.

The natural inference has been that the prairies were much modified by the grazing of animals and the fires of primitive man, and this has been reinforced by estimates of the population of each. Seton (1929) concludes that the original number of bison was about 60 million with a probable reduction to 40 million by 1800, and that both the antelope and white-tailed deer were equally abundant, while elk and mule-deer each amounted to not more than 10 million at the maximum. However, these were distributed over a billion or two acres, and the average density was probably never more than a score to the square mile. Estimates of the Indian tribes show the greatest divergence, but it seems improbable that the total population within the grassland ever exceeded a half million. The general habit of migration among the animals further insured that serious effects from overgrazing and trampling were but local or transitory, while the influence of fires set by the Indians was even less significant in modifying the plant cover. As to the forests, those of the north-west were still primeval and in the east they were yet to be changed over wide areas by lumbering and burning on a large scale.

## THE CLIMAX CONCEPT

The idea of a climax in the development of vegetation was first suggested by Hult in 1885 and then was advanced more or less independently by several investigators during the next decade or so (cf. Clements, 1916; Phillips, 1935). It was applied to a more or less permanent and final stage of a particular succession and hence one characteristic of a restricted area. The concept of the climax as a complex organism inseparably connected with its climate and often continental in extent was introduced by Clements (1916). According to this view, the climax constitutes the major unit of vegetation and as such forms the basis for the natural classification of plant communities. The relation between climate and climax is considered to be the paramount one, while the intimate



bond between the two is emphasized by the derivation of the terms from the same Greek root. In consequence, under this concept climax is invariably employed with reference to the climatic community alone, namely, the formation or its major divisions.

At the outset it was recognized that animals must also be considered members of the climax, and the word *biome* was proposed for the purpose of laying stress upon the mutual roles of plants and animals (Clements, 1916*b*; Clements and Shelford, 1936). With this went the realization that the primary relations to the habitat or *ecce* were necessarily different by virtue of the fact that plants are producents and animals consuments. On land, moreover, plants constitute the fixed matrix of the biome in direct connection with the climate, while the animals bear a dual relation, to plants as well as to climate. The outstanding effect of the one is displayed in reaction upon the *ecce*, of the other in coaction upon plants, which constitutes the primary bond of the biotic community.

Because of its emphasis upon the climatic relation, the term climax has come more and more to replace the word formation, which is regarded as an exact synonym, and this process may have been favored by a tendency to avoid confusion with the geological use. The designation "climatic formation" has now and then been employed, but this is merely to accentuate its nature and to distinguish it from less definite usages. Furthermore, climax and biome are complete synonyms when the biotic community is to be indicated, though climax will necessarily continue to be employed for the matrix when plants alone are considered.

#### NATURE OF THE CLIMAX

This theme has been developed in considerable detail in earlier works (Clements, 1916, 1920, 1928; Weaver and Clements, 1929), as well as in a recent comprehensive treatment by Phillips (1935), and hence a summary account of the major features will suffice in the present place. These may be conveniently grouped under the following four captions, i.e. unity, stabilization and change, origin and relationship, and objective tests.

#### *Unity of the climax*

The inherent unity of the climax rests upon the fact that it is not merely the response to a particular climate, but is at the same time the expression and the indicator of it. Because of extent, variation in space and time, and the usually gradual transition into adjacent climates, to say nothing of the human equation, neither physical nor human measures of a climate are adequately satisfactory. By contrast, the visibility, continuity, and sessile nature of the plant community are peculiarly helpful in indicating the fluctuating limits of a climate, while its direct response in terms of food-making, growth and life-form provides the fullest possible integration of physical factors. Naturally,

both physical and human values have a part in analyzing and in interpreting the climate as outlined by the climax, but these can only supplement and not replace the biotic indicators.

It may seem logical to infer that the unity of both climax and climate should be matched by a similar uniformity, but reflection will make clear that such is not the case. This is due in the first place to the gradual but marked shift in rainfall or temperature from one boundary to the other, probably best illustrated by the climate of the prairie. In terms of precipitation, the latter may range along the parallel of  $40^{\circ}$  from nearly 40 in. at the eastern edge of the true prairie to approximately 10 in. at the western border of the mixed grassland, or even to 6 in. in the desert plains and the Great Valley of California. Such a change is roughly 1 in. for 50 miles and is regionally all but imperceptible. The temperature change along the 100th meridian from the mixed prairie in Texas to that of Manitoba and Saskatchewan is even more striking, since only one association is concerned. At the south the average period without killing frost is about 9 months, but at the north it is less than 3, while the mean annual temperatures are  $70$  and  $33^{\circ}$  F. respectively. The variation of the two major factors at the extremes of the climatic cycle is likewise great, the maximum rainfall not infrequently amounting to three to four times that of the minimum.

The visible unity of the climax is due primarily to the life-form of the dominants, which is the concrete expression of the climate. In prairie and steppe, this is the grass form, with which must be reckoned the sedges, especially in the tundra. The shrub characterizes the three scrub climaxes of North America, namely, desert, sagebrush, and chaparral, while the tree appears in three subforms, coniferous, deciduous, and broad-leaved evergreen, to typify the corresponding boreal, temperate, and tropical climaxes. The life-form is naturally reflected in the genus, though not without exceptions, since two or more forms or subforms, herb or shrub, deciduous or evergreen, annual or perennial, may occur in the same genus. Hence, the essential unity of a climax is to be sought in its dominant species, since these embody not only the life-form and the genus, but also denote in themselves a definite relation to the climate. Their reactions and coactions are the most controlling both in kind and amount, and thus they determine the conditions under which all the remaining species are associated with them. This is true to a less degree of the animal influents, though their coactions may often be more significant than those of plants.

#### *Stabilization and change*

Under the growing tendency to abandon static concepts, it is comprehensible that the pendulum should swing too far and change be overstressed. This consequence is fostered by the fact that most ecological studies are carried out in settled regions where disturbance is the ruling process. As a result, the

climax is badly fragmented or even absent over wide areas and subseres are legion. In all such instances it is exceedingly difficult or entirely impossible to strike a balance between stability and change, and it becomes imperative to turn to regions much less disturbed by man, where climatic control is still paramount. It is likewise essential to employ a conceivable measure of time, such as can be expressed in human terms of millennia rather than in eons. No student of past vegetation entertains a doubt that climaxes have evolved, migrated and disappeared under the compulsion of great climatic changes from the Paleozoic onward, but he is also insistent that they persist through millions of years in the absence of such changes and of destructive disturbances by man. There is good and even conclusive evidence within the limitations of fossil materials that the prairie climax has been in existence for several millions of years at least and with most of the dominant species of to-day. This is even more certainly true of forests on the Pacific Coast, owing to the wealth of fossil evidence (Chaney, 1925, 1935), while the generic dominants of the deciduous forests of the Dakota Cretaceous and of to-day are strikingly similar.

It can still be confidently affirmed that stabilization is the universal tendency of all vegetation under the ruling climate, and that climaxes are characterized by a high degree of stability when reckoned in thousands or even millions of years. No one realizes more clearly than the devotee of succession that change is constantly and universally at work, but in the absence of civilized man this is within the fabric of the climax and not destructive of it. Even in a country as intensively developed as the Middle West, the prairie relicts exhibit almost complete stability of dominants and subdominants in spite of being surrounded by cultivation (cf. Weaver and Flory, 1934). It is obvious that climaxes display superficial changes with the season, year or cycle, as in aspection and annuation, but these modify the matrix itself little or not at all. The annuals of the desert may be present in millions one year and absent the next, or one dominant grass may seem prevailing one season and a different one the following year, but these changes are merely recurrent or indeed only apparent. While the modifications represented by bare areas and by seres in every stage are more striking, these are all in the irresistible process of being stabilized as rapidly as the controlling climate and the interference of man permit.

In brief, the changes due to aspection, annuation or natural coaction are superficial, fleeting or periodic and leave no permanent impress, while those of succession are an intrinsic part of the stabilizing process. Man alone can destroy the stability of the climax during the long period of control by its climate, and he accomplishes this by fragments in consequence of a destruction that is selective, partial or complete, and continually renewed.

*Origin and relationship*

Like other but simpler organisms, each climax not only has its own growth and development in terms of primary and secondary succession, but it has also evolved out of a preceding climax. In other words, it possesses an ontogeny and phylogeny that can be quantitatively and experimentally studied, much as with the individuals and species of plants and animals (*Plant Succession*, 1916, pp. 181, 342). Out of the one has come widespread activity in the investigation of succession, while interest in the other lingers on the threshold, chiefly because it demands a knowledge of the climaxes of more than one continent. With increasing research in these, especially in Europe and Asia, it will be possible to test critically the panclimaxes already suggested (Clements, 1916, 1924, 1929), as well as to determine the origin and relationships of the constituent formations.

This task will also require the services of paleo-ecology for the reconstruction of each eoclimax, which has been differentiated by worldwide climatic changes into the existing units of the panclimax or panformation. As it is, there can be no serious question of the existence of a great hemispheric clisere constituted by the arctic, boreal, deciduous, grassland, subtropical and tropical panclimaxes. Desert formations for the most part constitute an exception and may well be regarded as endemic climaxes evolved in response to regional changes of climate (Clements, 1935).

It is a significant fact that the boreal formations of North America and Eurasia are more closely related than the coniferous ones of the former, but this seeming anomaly is explained by the greater climatic differences that have produced the forests of the Petran and Sierran systems. The five climaxes concerned are relatively well known, and it is possible to indicate their relationships with some assurance, and all the more because of their parallel development on the two great mountain chains. In the case of deciduous forest and grassland, only a single formation of each is present in North America, and the problem of differentiation resolves itself into tracing the origin and relationship of the several associations. It has been suggested that the mixed prairie by virtue of its position, extent and common dominants represents the original formation in Tertiary times, an assumption reinforced by its close resemblance to the steppe climax (Clements, 1935). It is not improbable that the mixed hardwoods of the southern Appalachians bear a similar relation to the associations of the modern deciduous forest (Braun, 1935).

*Tests of a climax*

As has been previously indicated, the major climaxes of North America, such as tundra, boreal and deciduous forest, and prairie, stand forth clearly as distinct units, in spite of the fact that the prairie was first regarded as comprising two formations, as a consequence of the changes produced by over-

grazing. The other coniferous and the scrub climaxes emerge less distinctly because of the greater similarity of life-form within each group, and hence it is necessary to appeal to criteria derived from the major formations just mentioned. This insures uniformity of basis and a high degree of objectivity, both of which are qualities of paramount importance for the natural classification of biomes. In fact, entire consistency in the application of criteria is the best warrant of objective results, though this is obviously a procedure that demands a first-hand acquaintance with most if not all the units concerned and over a large portion of their respective areas.

The primary criterion is that afforded by the vegetation-form, as is illustrated by the four major climaxes. The others of each group, such as coniferous forest or scrub, are characterized also by the same form in the dominants, but this is not decisive as between related climaxes and hence recourse must be taken to the other tests. The value of the life-form is most evident where two climaxes of different physiognomy are in contact, as in the case of the lake forest of pine-hemlock and the deciduous forest of hardwoods. The static view would make the hemlock in particular a dominant of the deciduous formation, but the evidence derived from the vegetation-form is supported by that of phylogeny and by early records of composition and timber-cut to show that two different climaxes are concerned. Secondary forms or subforms rarely if ever mark distinctions between climaxes, but do aid in the recognition of associations. This is well exemplified by the tall, mid and short grasses of the prairie and somewhat less definitely by the generally deciduous character of the Petran chaparral and the typically evergreen nature of the Sierran.

As would be expected, the most significant test of the unity of a formation is afforded by the presence of certain dominant species through all or nearly all of the associations, but often not in the role of dominants by reason of reduced abundance. Here again perhaps the best examples are furnished by prairie and tundra, though the rule applies almost equally well to deciduous forest and only less so to coniferous ones because of a usually smaller number of dominants. For the prairie, the number of such species, or *perdominants*, found in all or all but one or two of the five associations is eight, namely, *Stipa comata*, *Agropyrum smithi*, *Bouteloua gracilis*, *Sporobolus cryptandrus*, *Koeleria cristata*, *Elymus sitanion*, *Poa scabrella* and *Festuca ovina*. Even when a species is lacking over most of an association, as in the case of *Stipa comata* and the true prairie, it may be represented by a close relative, such as *S. spartea*, which is probably no more than a mesic variety of it. As to the three associations of the deciduous forest, a still larger number of dominant species occur to some degree in all; the oaks comprise *Quercus borealis*, *velutina*, *alba*, *macrocarpa*, *coccinea*, *muhlenbergi*, *stellata* and *marilandica*, and the hickories, *Carya ovata*, *glabra*, *alba* and *cordiformis*.

It was the application of this test by specific dominants that led to the recognition of the two climaxes in the coniferous mantle of the Petran and

Sierran cordilleras. The natural assumption was that such a narrow belt could not contain more than one climax, especially in view of its physiognomic uniformity, but this failed to reckon with the great climatic differences of the two portions and the corresponding response of the dominants. The effect of altitude proved to be much more decisive than that of region, dominants common to the montane and subalpine zones being practically absent, though the rule for the same zone in each of the two separate mountain systems. Long after the presence of two climaxes had been established, it was found that Sargent had anticipated this conclusion, though in other terms (1884, p. 8).

As would be inferred, the dominants of related associations belong to a few common genera for the most part. Thus, there are a dozen species of *Stipa* variously distributed as dominants through the grassland, nearly as many of *Sporobolus*, *Bouteloua* and *Aristida*, and several each of *Poa*, *Agropyrum*, *Elymus*, *Andropogon*, *Festuca* and *Muhlenbergia*. In the deciduous forest, *Quercus*, *Carya* and *Acer* are the great genera, and for the various coniferous ones, *Pinus*, *Abies* and *Picea*, with species of *Tsuga*, *Thuja*, *Larix* and *Juniperus* hardly less numerous.

The perennial forbs that play the part of subdominants also possess considerable value in linking associations together, and to a higher degree in the deciduous forest than in the prairie, owing chiefly to the factors of shade and protection. Over a hundred subdominants belonging to two score or more of genera, such as *Erythronium*, *Dicentra*, *Trillium*, *Aquilegia*, *Arisaema*, *Phlox*, *Uvularia*, *Viola*, *Impatiens*, *Desmodium*, *Helianthus*, *Aster* and *Solidago*, range from Nova Scotia or New England beyond the borders of the actual climax to Nebraska and Kansas. Across the wide expanse of the prairie climax, species in common are only exceptional, these few belonging mostly to the composites, notably *Grindelia squarrosa*, *Gutierrezia sarothrae*, *Artemisia dracuncululus* and *vulgaris*. On the other hand, the number of genera of subdominants found throughout the grassland is very large.

The greater mobility of the larger mammals in particular renders animal influents less significant than plants as a criterion, but several of these possess definite value and the less mobile rodents even more. The antelope and bison are typical of the grassland climax, the first being practically restricted to it, while jack-rabbits, ground-squirrels and kangaroo-rats are characteristic dwellers in the prairie, as is their chief foe, the coyote.

The remaining criteria are derived from development directly or indirectly, though this is less evident in the case of the ecotone between two associations. Here the mixing of dominants and subdominants indicates their general similarity in terms of the formation, within which range their preferences assign them to different associations. The evidence from primary succession is of value only in the later stages as a rule, since initial associates like the reed-swamp may occur in several climaxes. With subseres, however, all or nearly all the stages are related to the particular climax and such seres denote a

corresponding unity in development. This is especially true of all subclimaxes and most evidently in the case of those due to fire. More significant still are postclimaxes in both grassland and forest. For example, the associates of species of *Andropogon*, which is subclimax to the oak-hickory forest, constitutes a postclimax to five out of the six associations of the prairie. On the other hand, the community of *Ulmus*, *Juglans*, *Fraxinus*, etc., found on flood-plains through the region of deciduous forest, forms a common subclimax to the three associations.

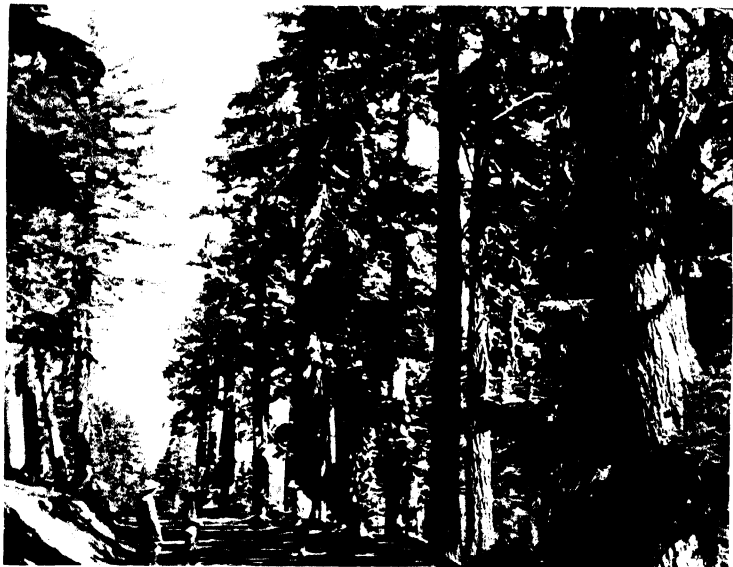
In addition to such ontogenetic criteria, phylogeny supplies tests of even greater value. This is notably the case with the two associations of the montane and subalpine coniferous forests of the west, though perhaps the most striking application of this criterion is in connection with the lake forest of pine-hemlock. Though the concrete evidence for such a climax recurs constantly through the region of the Great Lakes to the Atlantic, it is fragmentary and there is no evident related association to the westward. However, the four genera are represented by related species in the two regions, namely, *Pinus strobus* by *P. monticola*, *P. banksiana* by *P. contorta*, *Tsuga canadensis* by *T. heterophylla*, *Larix laricina* by *L. occidentalis*, and *Thuja occidentalis* by *T. plicata*, though the last two genera have changed from a subclimax role in the east to a climax one in the west. As suggested earlier, phylogenetic evidence of still more direct nature is supplied by the mixed prairie with the other enclosing associations and by the remnants of a virgin deciduous forest that exhibits a similar genetic and spatial relation to the associations of this climax (cf. Braun, 1935).

Finally, it is clear that any test will gain in definiteness and accuracy of application whenever dependable records are available with respect to earlier composition and structure. These may belong entirely to the historical period, as in the case of scientific reports or land surveys, they may bridge the gap between the present and the past as with pollen statistics, or they may reach further back into the geological record, as with leaf-impressions or other fossils (Chaney, 1925, 1933; Clements, 1936). Two instances of the scientific record that are of the first importance may be given as examples. The first is the essential recognition by Sargent of the pine-hemlock climax under the name of the northern pine belt (1884), at a time when relatively little of this had been logged, by contrast with 90 per cent. or more at present (cf. also Bromley, 1935). The second is an account, discovered and communicated by Dr Vestal, of the prairies of Illinois as seen by Short in ca. 1840. This is of heightened interest since its discovery followed little more than a year after repeated field trips had led to the conclusion that all of Iowa, northern Missouri and most of Illinois were to be assigned to the true prairie,<sup>1</sup> a decision

<sup>1</sup> The true prairie is characterized by the three eudominants, *Stipa spartea*, *Sporobolus asper* and *S. heterolepis*. The presence of tall-grasses in it to-day, particularly *Andropogon furcatus* and *nutans*, is the mark of the disclimax due to the varied disturbances associated with settlement.







Phot. 1. Sierran subalpine climax: Consociation of *Tsuga mertensiana*; Crater Lake, Oregon.



Phot. 2. Proclimax of Sagebrush (*Artemisia tridentata*), a disclimax due to overgrazing of mixed prairie; climatically a preclimax.

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confirmed for Illinois by Short's description, and supported by the more general accounts of Bradbury (*ca.* 1815) and Greeley (1860).

#### CLIMAX AND PROCLIMAX

##### *Essential relations*

In accordance with the view that development regularly terminates in the community capable of maintaining itself under a particular climate, except when disturbance enters, there is but one kind of climax, namely, that controlled by climate. This essential relation is regarded as not only inherent in all natural vegetation, but also as implicit in the cognate nature of the two terms. While it is fully recognized that succession may be halted in practically any stage, such communities are invariably subordinate to the true climax as determined by climate alone. From the very meaning of the word, there can not be climaxes scattered along the developmental route with a genuine climax at the end. There is no intention to question the reality of such pauses, but only to emphasize the fact that they are of a different order from the climax.

While it is natural to express new ideas by qualifying an old term, this does not conduce to the clearest thinking or the most accurate usage. Even more undesirable is the fact that the meaning of the original word is gradually shifted until it becomes either quite vague or hopelessly inclusive. At the hands of some, climax has already suffered this fate, and fire, disease, insects, and human disturbances of all sorts are assumed to produce corresponding climaxes (*cf.* Chapman, 1932). On such an assumption corn would constitute one climax, wheat another, and cotton a third, and it would then become imperative to begin anew the task of properly analyzing and classifying vegetation.

In the light of two decades of continued analysis of the vegetation of North America, as well as the application of the twin concepts of climax and complex organism by workers in other portions of the globe and the strong support brought to them by the rise of emergent evolution and holism (Phillips, 1935), the characterization of the climax as given in *Plant Succession*, in 1916, still appears to be both complete and accurate. "The unit of vegetation, the climax formation, is an organic entity. As an organism, the formation arises, grows, matures and dies. Its response to the habitat is shown in processes or functions and in structures that are the record as well as the result of these functions. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development. The life-history of a formation is a complex but definite process, comparable in its chief features with the life-history of an individual plant. The climax formation is the adult organism, of which all initial and medial stages are but stages of development.... A formation, in short, is the final stage of vegetational development in a climatic unit. It is the climax community of a succession that terminates in the highest life-form possible in the climate concerned."

To-day this statement would need modification only to the extent of substituting "biome" for climax or formation and "biotic" for vegetational. This characterization has recently been annotated and confirmed by Phillips' masterly discussion of climax and complex organism, as cited above, a treatise that should be read and digested by everyone interested in the field of dynamic ecology and its wide applications.

### *Proclimaxes*

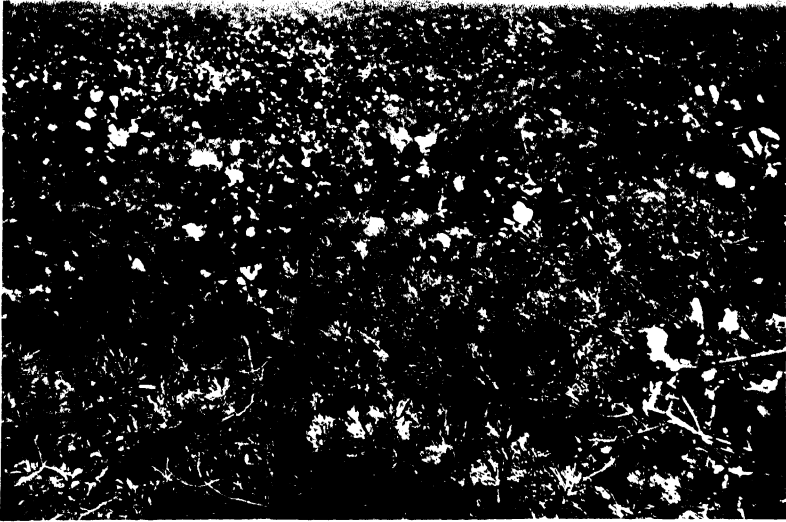
As a general term, proclimax includes all the communities that simulate the climax to some extent in terms of stability or permanence but lack the proper sanction of the existing climate. Certain communities of this type were called potential climaxes in *Plant Succession* (p. 108; 1928, p. 109), and two kinds were distinguished, namely, preclimax and postclimax. To avoid proposing a new term in advance of its need, subclimax was made to do double duty, denoting both the subfinal stage of succession, as well as apparent climaxes of other kinds. This dual usage was criticized by Godwin (1929, p. 144) and partially justified by Tansley in an appended note on the ground just given. However, this discussion made it evident that a new term was desirable and proclimax was accordingly suggested (Clements, 1934). While this takes care of the use of subclimax in the second sense noted above, it is better adapted by reason of its significance to apply to all kinds of subpermanent communities other than the climax proper. However, there is still an important residuum after subclimax, preclimax and postclimax have been recognized, and it is proposed to call these *disclimaxes*, as indicated later.

The proclimax may be defined as any more or less permanent community resembling the climax in one or more respects, but gradually replaceable by the latter when the control of climate is not inhibited by disturbance. Besides its general function, it may be used as a synonym for any one of its divisions, as well as in cases of doubt pending further investigation, such as in water climaxes. The four types to be considered are subclimax, disclimax, preclimax and postclimax.

### *Subclimax*

As the stage preceding the climax in all complete seres, primary and secondary, the subclimax is as universal as it is generally well understood. The great majority of such communities belong to the subsere, especially that following fire, owing to the fact that disturbance is to-day a practically constant feature of most climaxes. Fire and fallow are recurrent processes in cultivated regions generally and they serve to maintain the corresponding subsere until protection or conversion terminates the disturbance. Though the subclimax is just as regular a feature of priseres, these have long ago ended in the climax over most of the climatic area and the related subclimax communities are consequently much restricted in size and widely scattered. Smallness is





Phot. 3. Fire subclimax of dwarf *Pinus* and *Quercus*; the "Plains",  
New Jersey Pine-barrens.



Phot. 4. Subclimax of consociates of *Aristida purpurea* in field  
abandoned 15 years; Great Plains.

naturally a characteristic of nearly all subclimaxes, the chief exceptions being due to fire or to fire and logging combined, but by contrast they are often exceedingly numerous.

Because of its position in the succession, the subclimax resembles the preclimax in some respects and in a few instances either term may be properly applied. The distinction between subclimax and disclimax presents some difficulty now and then, as the amount of change necessary to produce the latter may be a matter of judgment. This arises in part also from the structural diversity of formation and association, as a consequence of which the dominants of a particular type of subserie vary in different areas. When there is but a single dominant, as in many burn subclimaxes, no question ensues, but if two or more are present, the decision between subclimax and disclimax may be less simple, as is not infrequent in scrub and grassland.

Examples of the subclimax are legion, the outstanding cases being mostly due to fire, alone or after lumbering or clearing. Most typical are those composed of "jack-pines" or species with closed cones that open most readily after fire. Each great region has at least one of these, e.g. *Pinus rigida*, *virginiana* and *echinata* in the east, *P. banksiana* in the north, *P. murrayana* in the Rocky Mountains, and *P. tuberculata*, *muricata* and *radiata* on the Pacific Slope. *Pinus palustris* and *taeda* play a similar role in the "piney" woods of the Atlantic Gulf region, as does *Pseudotsuga taxifolia* in the north-west. The characteristic subclimaxes of the boreal forest are composed of aspen (*Populus tremuloides*), balsam-poplar (*P. balsamifera*), and paper-birch (*Betula papyrifera*), either singly or in various combinations. Aspen also forms a notable subclimax in the Rocky Mountains, for the most part in the subalpine zone. Prisere subclimaxes are regular features of bogs and muskeags throughout much or all of the boreal and lake forests, the three dominants being *Larix laricina*, *Picea mariana* and *Thuja occidentalis*, often associated as zonal consocieties. Where pines are absent in the region of the deciduous forest, two xeric oaks, *Quercus stellata* and *marilandica*, may constitute a subclimax, and this role is sometimes assumed by small trees, *Sassafras*, *Diospyrus* and *Hamamelis* being especially important.

Subclimaxes in the grassland are composed largely of tall-grasses, usually in the form of a consocieties. In the true prairie, this part is taken by *Spartina cynosuroides* and in the desert plains by *Sporobolus wrightii*, while *Elymus condensatus* plays a similar role in the mixed prairie and in portions of the bunch-grass prairies. The function of the tall Andropogons is more varied; they are typically postclimax rather than subclimax, though they maintain the latter relation along the fringe of the oak-hickory forest and in oak openings. They occupy a similar position at the margin of the pine subclimax in Texas especially, and hence they are what might be termed "sub-subclimax" in such situations. Beyond the forest and in association with *Elionurus*, *Trachypogon*, etc., they appear to constitute a faciation of the coastal prairie. Chaparral

proper is to be regarded as a climax, but with a change of species it extends into the montane and even the subalpine zone and there constitutes a fire subclimax. In the foothills of southern California, the coastal sagebrush behaves in like manner where it lies in contact with the chaparral.

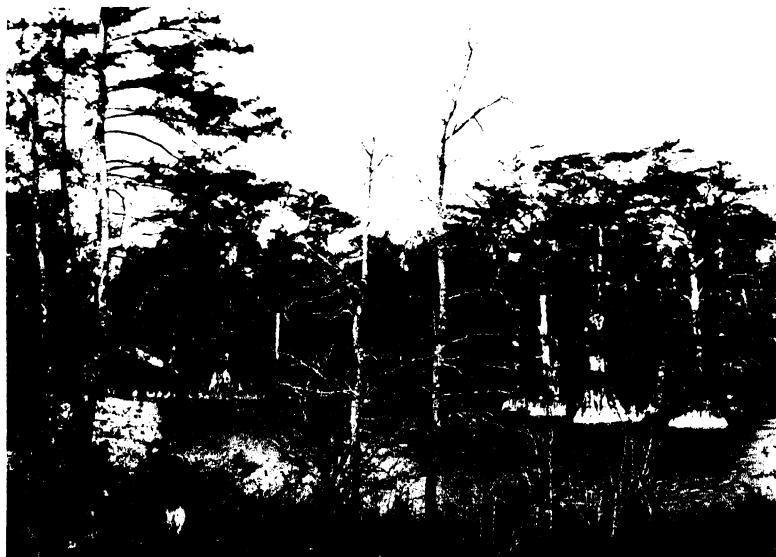
The disposition of seral stages below the subclimax that exhibit a distinct retardation or halt for a longer or shorter period is a debatable matter. It is entirely possible to include them among subclimaxes, but this would again fail in accuracy and definiteness and hence lead to confusion. The decision may well be left to usage by providing a term for such seral or sub-subclimax communities as persist for a long or indefinite period because of continued or recurrent edaphic control or human disturbance. By virtue of its significance, brevity and accord with related terms, the designation "serclimax" is suggested, with the meaning of a seral community usually one or two stages before the subclimax, which persists for such a period as to resemble the climax in this one respect. For reasons of brevity and agreement, the connecting vowel is omitted, but the *e* remains long as in *sere*.

For the most part, serclimaxes are found in standing water or in saturated soils as a consequence of imperfect drainage. The universal example is the reed-swamp with one or more of several consociates, such as *Scirpus*, *Typha*, *Zizania*, *Phragmites* and *Glyceria*: this is typical of the lower reaches of rivers, of deltas and of certain kinds of lakes, the great tule swamps of California affording outstanding instances. Another type occurs in coastal marshes in which *Spartina* is often the sole or major dominant, while sedge-swamps have a wider climatic range but are especially characteristic of northern latitudes and high altitudes. The Everglades of Florida dominated by *Cladium* constitute perhaps the most extensive example of the general group, though *Carex* swamps often cover great areas and the grass *Arundinaria* forms jungle-like cane-brakes through the south. Among woody species, *Salix longifolia* is an omnipresent consociate of sand-bars and river-sides, but the most unique exemplar is the cypress-swamp of the south, typified by *Taxodium*. In boreal and subalpine districts the distinctive serclimax is the peat-bog, moor or muskeg, more or less regularly associated with other seral communities of *Carex* and usually of *Larix* or *Picea* also in the proper region.

Frequent burning may retard or prevent the development of the normal fire subclimax and cause it to be replaced by a preceding stage. This may be a scrub community or one kept in the shrub form by repeated fires, but along the Atlantic and Gulf Coasts it is usually one of *Andropogon virginicus*, owing to its sufferance of burning. The so-called "balds" of the southern Appalachians are seral communities of heaths or grasses initiated and maintained primarily by fire. Finally, there are serclimaxes of weeds, especially annuals, in cultivated districts, and a somewhat similar community of native annuals is characteristic of wide stretches in the desert region.







Phot. 5. Serclimax of *Taxodium*, *Nyssa* and *Quercus* forming a cypress swamp; Paris, Arkansas.



Phot. 6. Disclimax of *Bouteloua*, *Muhlenbergia* and *Opuntia*, due to overgrazing of mixed prairie, Great Plains.

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*Disclimax*

As with the related concepts, the significance of this term is indicated by a prefix, *dis-*, denoting separation, unlikeness or derogation, much as in the Greek *dys*, poor, bad. The most frequent examples of this community result from the modification or replacement of the true climax, either as a whole or in part, or from a change in the direction of succession. These ensue chiefly in consequence of a disturbance by man or domesticated animals, but they are also occasionally produced by mass migration. In some cases, disturbance and the introduction of alien species act together through destruction and competition to constitute a quasi-permanent community with the general character of the climax. This type is best illustrated by the *Avena-Bromus* disclimax of California, which has all but completely replaced the bunch-grass prairie.<sup>1</sup> A similar replacement by *Bromus tectorum* has more recently taken place over large areas of the Great Basin, while *Poa pratensis* has during the last half-century steadily invaded the native hay-fields and pastures of the true prairie, an advance first noted by Bradbury in 1809. An even more striking phenomenon is the steadily increasing dominance of *Salsola* over range and crop land in the west, and this is imitated by *Sisymbrium* and *Lepidium* in the north-west. It is obvious that all cultivated crops belong in the same general category, but this point hardly requires consideration.

Probably the example most cited in North America is that of the short-grass plains, which actually represent a reduction of the mixed prairie due to overgrazing, supplemented by periodic drouth. Over most of this association, the mid-grasses, *Stipa*, *Agropyrum*, etc., are still in evidence, though often reduced in abundance and stature, but in some areas they have been practically eliminated. Similar though less extensive partial climaxes of short-grasses characterise pastures in the true and both pasture and range in the coastal prairie, the dominants regularly belonging to *Bouteloua*, *Buchloe* or *Hilaria*. Of essentially the same nature is the substitution of annual species of *Bouteloua*

<sup>1</sup> The grassland climax of North America comprises six well-marked associations (*Plant Indicators*, 1920; *Plant Ecology*, 1929). The mixed prairie, so-called because it is composed of both mid-grasses and short-grasses, is more or less central to the other five and is regarded as ancestral to them. To the east along the Missouri and Mississippi Rivers, it has become differentiated into the true prairie formed by other species of mid-grasses pertaining mostly to the same genera, and this unit is flanked along the western margin of the deciduous forest by a proclimax of tall grasses, chiefly *Andropogon*. Southward the true prairie is replaced by coastal prairie, which in the main occupies the Gulf region of Texas and Mexico and is constituted by similar dominants but of different species. The desert plains are characterized primarily by species of *Bouteloua* and *Aristida*, which range from western Texas to the edge of the deserts of Mexico and Arizona. In the north-west the short-grasses disappear and the Palouse prairie of eastern Washington and adjacent regions is formed by mid-grasses of the bunch-grass life-form, among which *Agropyrum spicatum* is the eudominant. The same life-form signalizes the California prairie, found from the northern part of the state southward into Lower California, but its especial character is derived from endemic species of *Stipa*. As indicated in the discussion, the short-grass plains, composed of *Bouteloua*, *Buchloe*, and *Carex*, are not climatic in nature, and this statement applies likewise to the tall-grass meadows of *Andropogon* mentioned above.

and *Aristida* in the desert plains for perennial ones of the same genera, which is a case of short-grasses being followed by still shorter ones.

In other instances, the effect of disturbance is to produce a community with the appearance of a postclimax, when the life-form concerned is that of an undershrub or tall grass. This is notably the case in the mixed prairie when overgrazing is carried to the point of breaking up the short-grass sod and permitting the dominance of *Artemisia frigida* or *Gutierrezia sarothrae*. In essence, the wide extension of sagebrush (*Artemisia tridentata*) and of creosote-bush (*Larrea tridentata*) is the same phenomenon, though each of these is a climax dominant in its own region. In the case of *Opuntia*, the peculiar life-form suggests an important difference, but the numerous species behave in all significant respects like other shrubs, though with the two advantages of spines and ready propagation.

The communities of tall-grasses formed by species of *Andropogon* originally presented some difficulty, since these naturally have all the appearance of a postclimax to the prairie. Probably the greater number are to be assigned to this type, but the evidence from reconnaissance and record indicates that in the true prairie and especially the eastern portion, *Andropogon furcatus* in particular now constitutes a disclimax due to pasturing, mowing and in some measure to fire also (Clements, 1933). A characteristic disclimax in miniature is to be found in the "gopher gardens" of the alpine tundra, where coaction and reaction have removed the climax dominants of sedges and grasses to make place for flower gardens of perennial forbs. "Towns" of prairie-dogs and kangaroo-rats often produce similar but much more extensive communities.

Selective cutting not infrequently initiates disclimaxes, as may likewise the similar action of other agents such as fire or epidemic disease. The most dramatic example is the elimination of the chestnut (*Castanea dentata*) from the oak-chestnut canopy, but of even greater importance has been the extreme reduction and fragmentation of the lake forest through the overcutting of white pine. Finally, what is essentially a disclimax may result from climatic mass migration, such as in the Black Hills of South Dakota has brought together *Pinus ponderosa* from the montane climax of the Rocky Mountains and *Picea canadensis* from the boreal forest.

#### *Preclimax and postclimax*

These related concepts were first advanced in *Plant Succession* (1916, 1928) and have since been discussed in *Plant Ecology* (1929) and in the organisation of the relict method (1934). They are both direct corollaries of the principle of the clisere, the spatial series of climaxes that are set in motion by a major climatic shift, such as that of the glacial epoch with its opposite phases. The clisere is most readily comprehended in the case of high ranges or summits, such as Pikes Peak where the entire series of climaxes is readily visible, and is what Tournefort described on Mount Ararat in his famous journey of 1700.

However, this is but an expression of the continental clisere in latitude, which achieves perhaps its greatest regularity in North America. A similar relation is characteristic of the longitudinal disposition of climaxes in the temperate zone between the two oceans, the portion from deciduous forest through prairie to desert being the most uniform.

With the exception of the two extremes, arctalpine and tropical, each climax has a dual role, being preclimax to the contiguous community of so-called higher life-form and postclimax to that of lower life-form. This may be illustrated by the woodland climax, which is postclimax to grassland and preclimax to montane forest. The arctic and alpine tundras exhibit only the preclimax relation, to boreal and subalpine forest respectively, since a potential lichen climax attains but incomplete expression northward or upward. While the general primary relation is one of water in terms of rainfall and evaporation, temperature constantly enters the situation and at the extremes may be largely controlling, as in the tundra especially. However, in our present imperfect knowledge of causal factors it is simpler and more definite to determine rank by position in the cliseral sequence, each community higher in altitude or latitude being successively preclimax to the preceding one. This relation is likewise entirely consistent in the clisere from deciduous forest to desert, as it is among the associations of the same climax, though in both these cases the zonal grouping may be more or less obscured.

Wherever concrete preclimaxes or postclimaxes occur, either between climaxes or within a single one, they are due to the compensation afforded by edaphic situations. The major examples of the latter are provided by valleys, especially gorges and canyons, long and steep slope-exposures, and by extreme soil-types such as sand and alkali. The seration is a series of communities produced by a graduated compensation across a valley and operating within a formation or through adjacent ones, while the ecocline embraces the differentiation brought about by shifting slope-exposures around a mountain or on the two sides of a high ridge. In the case of such soils as sand or gravel at one extreme and stiff clay at the other, the edaphic adjustment may sometimes appear contradictory. Thus, sand affords a haven for postclimax relicts in the dry prairie and for preclimax ones in the humid forest region, while the effect of heavy soils is just the reverse. However, this is readily intelligible when one recalls the peculiar properties of such soils in terms of absorption, chresard and evaporation (Clements, 1933).

### *Preclimax*

Since they occupy the same general antecedent position with respect to the climax, it is necessary to distinguish with some care between subclimax and preclimax, especially in view of the fact that they often exhibit the same life-form. However, this is not difficult when the priseres and subseres have been investigated in detail, as the actual composition and behavior of the two

communities are usually quite different. Moreover, in the first, reaction leads to the entry of the climax dominants with ultimate conversion, while in the second the compensation by local factors is rarely if ever to be overcome within the existing climate, short of man-made disturbance.

Preclimaxes are most clearly marked where two adjacent formations are concerned, either prairie and forest or desert and prairie. Examples of the first kind are found in the grassy "openings" and oak savannahs of the deciduous forest and in the so-called "natural parks" along the margin of the montane and boreal forests. They are also well developed on warm dry slope-exposures or xeroclines in the Rocky Mountains. In the one, compensation is usually afforded by a sandy or rocky soil, in the other by a local climate due to insolation. Desert climaxes regularly bear the proper relation to circumjacent grassland, but this is somewhat obscured by the shrub life-form, which would be expected to characterize the less xeric formation. This may be explained, however, by the wide capacity for adaptation shown by such major dominants as *Larrea tridentata* and *Artemisia tridentata*, a quality that is lacking in most of their associates. Left stranded as relict communities in desert plains and mixed prairie by the recession of the last dry phase, they have profited by the overgrazing of grasses to extend across a territory much larger than that in which they are climax. Here they have all the appearance of a postclimax, especially in the case of *Larrea*, which commonly attains a stature several times that found in the desert. However, since this is the direct outcome of disturbance in terms of grazing, it is better regarded as a disclimax, particularly since the climax grasses still persist in it to some degree.

Within the same formation, the more xeric associations or consociations are preclimax to the less xeric ones. This is the general relation between the oak-hickory and beech-maple associations of the deciduous forest, the former occupying in the latter the warmer drier sites produced by insolation or type of soil. A similar relation may obtain in the case of faciatiions, the *Quercus stellata-marilandica* community often being a border of marginal preclimax to the more mesic oak-hickory faciatiions. Such preclimaxes naturally persist beyond the limits of the association proper as relicts in valleys or sandy soils and then assume the role of postclimaxes to the surrounding grassland, a situation strikingly exemplified in the "Cross Timbers" of Texas. In the montane forest of the Rockies, the consociation of *Pinus ponderosa* is preclimax to that of *Pseudotsuga taxifolia*, and a similar condition recurs in all forests where there is more or less segregation of consociations.

In the mixed prairie, fragments of the desert plains occur all along the margin as preclimaxes, the most extensive one confronting the Colorado Valley, where it is at the same time postclimax to the desert. The mixed prairie constitutes relicts of this type where it meets the true prairie. The most frequent examples are provided by *Bouteloua gracilis* and *Sporobolus cryptandrus*, though as with all the short-grasses in this role, grazing has played some part.





Phot. 7. Postclimax of *Quercus*, *Juglans*, *Ulmus*, *Fraxinus*, etc.,  
Canadian River, near Oklahoma City.



Phot. 8. Postclimax of tall-grasses, *Andropogon*, *Calamovilfa* and  
*Panicum* in sandhills; Thedford, Nebraska.

CLEMENTS—NATURE AND STRUCTURE OF THE CLIMAX

*Postclimax*

As a general rule, postclimax relicts are much more abundant than those that represent preclimaxes, owing in the first place to the secular trend toward desiccation in climate and in the second to the large number of valleys, sandhills and sandy plains, and escarpments in the grassland especially. Postclimaxes of oak-hickory and of their flood-plain associates, elm, ash, walnut, etc., are characteristic features of the true and mixed prairies, holding their own far westward in major valleys but limited as outliers on ridges and sandy stretches to the eastern edge. However, the compensation afforded by the last two is incomplete as a rule and the postclimax is typically reduced to the savannah type. The latter is an almost universal feature where forest, woodland or chaparral touches grassland, owing to the fact that shrinkage under slow desiccation operates gradually upon the density and size of individuals. Savannah is derived from the reduction of deciduous forest along the eastern edge of the prairie, of the aspen subclimax of the boreal forest along the northern, and of the montane pine consociation, woodland or chaparral on the western and southern borders, recurring again on the flanks of the Sierras and Coast Ranges in California. On the south, the unique ability of the mesquite (*Prosopis juliflora*) to produce root-sprouts after fire, its thorniness, palatable pods and resistant seeds have permitted it to produce an extensive savannah that often closely simulates a true woodland climax.

As would be expected, a point is reached in the reduction of rainfall westward in the prairie where sand no longer affords compensation adequate for trees. In general this is along the isohyet of 30 in. in the center and south, and of about 20 in. in the north. Southward from the parallel of 37° the further shrinkage of the oak savannah may be traced in the "shinry", which dwindles from four or five feet to dwarfs only "shin" high. With these are associated tall-grasses, principally *Andropogon* and *Calamovilfa* in the form *gigantea*. To the north of this line, the shin oaks are absent and the tall-grasses make a typical postclimax that extends into Canada, though the compensatory influence of sand is still sufficient to permit an abundance of such low bushes as *Amorpha*, *Ceanothus*, *Artemisia filifolia* and *Yucca*, as well as depauperate hackberry and aspen. In the vast sandhill area of central Nebraska, the tall-grass postclimax attains its best development, which is assumed to reflect the climate when the prairies were occupied by the *Andropogons* and their associates some millions of years ago. The gradual decrease to the rainfall of the present has led to the tall-grasses finding refuge in all areas of edaphic compensation, not only in sand but likewise on foothills and in valleys, and in addition along the front of the deciduous forest.



## STRUCTURE OF THE CLIMAX

*Community functions*

The nature of community functions and their relation to the structure of climax and sere have been discussed in considerable detail elsewhere (*Plant Succession*, 1916, 1928; *Plant Ecology*, 1929; *Bio-ecology*, 1936), and for the present purpose it may well suffice to emphasize the difference in significance between major or primary and minor or secondary functions. The former comprise aggregation, migration, ecesis, reaction, competition, cooperation, disoperation, and coaction, together with the resulting complexes, invasion and succession. Any one of these may have a profound effect upon community structure, but the driving force in the selection and grouping of life-forms and species resides chiefly in reaction, competition, and coaction. Migration deals for the most part with the movement and evolution of units under climatic compulsion, and succession with the development and regeneration of the climax in bare or denuded areas.

In contrast to these stands the group of minor functions that are concerned with numbers and appearance or visibility as it may be termed. The first is annuation, in accordance with which the abundance of any species may fluctuate from dry to wet phases of the various climatic cycles or the growth differ in terms of prominence, the two effects not infrequently being combined. For the grassland, a season of rainfall more or less extreme in either direction often emphasizes one dominant at the expense of others, though the balance is usually redressed by the following year, while in the desert in particular the swing in number of annuals may be from almost complete absence to seasonal dominance, again with one or few species taking the major role. Aspection is mainly the orderly procession of societies through each growing season, more or less modified by changes in number ensuing from annuation. Hibernation and estivation merely affect seasonal appearance and are forms of aspection, with the temporary suspension of coaction effects. While usually applied to the animal members of the biome, it is obvious that plants exhibit certain responses of similar nature. Diurnation is likewise best known in the case of animals, especially nocturnal ones, but it is exhibited also by the vertical movement of plankton and in different form by the opening and closing of flowers and the "sleep" movements of leaves.

*Roles of constituent species: dominants*

The abundant and controlling species of characteristic life-form were long ago termed dominants (Clements, 1907, 1916), this property being chiefly determined by the degree of reaction and effective competition. In harmony with the concept of the biome, it has become desirable to consider the role of animals likewise; since their influence is seen chiefly in coaction by contrast to the reaction of plants, the term *influent* has been applied to the important

species of land biomes (cf. Clements and Shelford, 1936). It is an axiom that the life-form of the dominant trees stamps its character upon forest and woodland, that of the shrub upon chaparral and desert, and the grass form on prairie, steppe and tundra. There are seral dominants as well as climax ones, and these give the respective impresses to the stages of prisere and subsere. Finally, there are considerable differences in rank or territory even among the dominants of each formation. The most important are those of wide range that bind together the associations of a climax; to these the term *perdominant* (*per*, throughout) may well be applied. In contrast to these stand the dominants more or less peculiar to each association, such as beech or chestnut in their respective communities and *Sporobolus asper* in the true and *Stipa comata* in the mixed prairie, for which *eudominant* may be employed.

*Subdominants* regularly belong to a life-form different from that of the dominants and are subject to the control of the latter in a high degree, as the name indicates. They are best exemplified by the perennial forbs, though biennials and annuals may serve as seral subdominants; all three may be actual dominants in the initial stages of succession and especially in the subsere. The term *codominant* has so far had no very definite status; it is hardly needed to call attention to the presence of two or more dominants, since this is the rule in all cases with the exception of consociation and consocieties. In contrast to the types mentioned stands a large number of secondary or accessory species that exhibit no dominance, which may be conveniently referred to as *edominants*, pending more detailed analysis.

### *Influents*

As indicated previously, the designation of *influent* is applied to the animal members of the biome by virtue of the influence or coaction they exert in the community. The significance of this effect depends much upon the life-form and to a large degree upon the size and abundance of the species as well, and is seen chiefly in the coactions involved in food, material, and shelter. *Influents* may be grouped in accordance with these properties, or they may be arranged with respect to distribution and role in climax or sere, or to time of appearance (Clements and Shelford, 1936). For general purposes it is perhaps most convenient to recognize subdivisions similar to those for dominants and with corresponding terms and significance. Thus, a *perfluent* would occur more or less throughout the formation, while the *eufluent* would be more or less typical or peculiar to an association. *Subfluents* would mark the next lower degree of importance, roughly comparable to that of subdominant, while minute or microscopic influents of still less significance might well be known as *vefluents*.

### *Climax and seral units*

No adequate analysis of vegetation or of the biome is possible without taking full account of development. As the first step, this involves a distinction between climax communities proper and those that constitute the

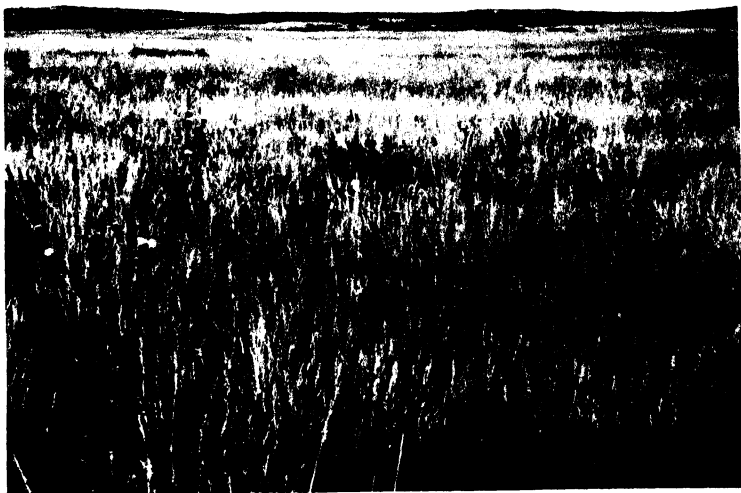
successional movement toward the final stages. The two groups differ in composition, stability, and type of control, but they agree in the possession of dominants, subdominants, and influents. These primary differences made it desirable to recognize two series of communities, viz. climax and seral and to propose corresponding terms, distinguished by the respective suffixes, *-ation* and *-ies* (Clements, 1916). These have gradually come into use as the feeling for dynamic ecology has grown and bid fair to constitute a permanent basis for all such studies. It is not supposed that they embrace all the units finally necessary for a complete system, but their constant application to the great climaxes of North America for nearly two decades indicates that they meet present needs in the matter of analysis.

Not all communities can be certainly placed in the proper category at the outset, but the number of doubtful cases is relatively small and few of these present serious difficulty under combined extensive and intensive research. This statement, however, presupposes an experience sufficiently wide and long to permit distinguishing between climaxes and the various types of proclimax, as well as recognizing the characteristic features of subclimaxes in particular. Comparative studies over a wide region are indispensable and the difficulties will disappear to the degree that this is achieved. While ecotones and mictia necessarily give rise to some questions in this connection, these in turn are resolved by investigations as extensive as they are detailed.

#### *Climax units*

In the organization of these, four types of descending rank and importance were distinguished within the formation, namely, association, consociation, society, and clan. Like the formation itself, the first two were based upon the dominant and its life-form, while the last were established upon the subdominant and its different life-form. It was recognized at the time that the association contained within itself other units formed by the dominants (cf. *Plant Indicators*, 1920, pp. 107, 276), and two further divisions, *faciation* and *lociation*, with corresponding seral ones, *facies* and *locies*, were suggested and submitted to Prof. Tansley for his opinion as to their desirability. These have been tested in the course of further field studies and have now and then been used in print, though the complete series was not published until 1932 (cf. Shelford, 1932). The climax group now comprises the following units, viz. association, consociation, faciation, lociation, society, and clan. At the beginning, it was intended to replace society by *sociation* for the sake of greater uniformity in terms, but the former had attained such usage that the idea was relinquished. However, the use of society in quite a different sense by students of social relations, especially among insects, again raises the question of the desirability of such a substitution, in view of the growing emphasis upon bioecology (cf. also Du Rietz, 1930; Rübel, 1930).





Phot. 9. Association of mixed prairie, *Stipa*, *Agropyrum*, *Bouteloua*, etc.: Monument, Colorado.



Phot. 10. Foothill faciation of the desert-plains association, *Bouteloua eriopoda*, *B. gracilis*, *B. hirsuta*, *B. filiformis*, etc.: Safford, Arizona.

CLEMENTS—NATURE AND STRUCTURE OF THE CLIMAX

*Association.*

Under the climax concept this represents the primary division of the biome or formation, and hence differs entirely from the generalized unit of the plant sociologists, for which the term *community* is to be preferred. Each biome consists regularly of two or more associations, though the lake forest and the desert scrub embody two apparent exceptions, each seeming to consist of one association only. However, these are readily explained by the fact that the western member of the former has been obscured by the expansion of montane and coast forests in the north-west, while one or more additional associations of the desert climax occur to the southward in Mexico, and apparently in South America also.

The number of associations in a particular formation is naturally determined by the number of primary differences and these in turn depend upon the presence of eudominants. Just as the unity of the formation rests upon the wide distribution of several major dominants or perdominants, so the association is also marked by one or more dominants peculiar to it, and often as well by differences in the rank and grouping of dominants held in common. Thus, in the true prairie association, the eudominants are *Stipa spartea*, *Sporobolus asper* and *heterolepis*; for the desert plains, *Bouteloua eriopoda*, *rothrocki* and *radicosa* and *Aristida californica*, while *Stipa comata* and *Buchloe* take a similar part in the mixed prairie. In the deciduous climax, the characteristic dominants of one association are supplied by the beech and hard maple, of a second by chestnut and chestnut-oak, though the oak-hickory association, of wider range and greater complexity, is comparatively poor in eudominants by contrast with the number of species.

The structural and phyletic relations of the associations of a climax are best illustrated by the grassland, which is the most highly differentiated of all North American formations, largely as an outcome of its great extent. The most extensive and varied unit is the mixed prairie, which occupies a generally median position with respect to the other five associations of this climax. Originally, it derived its dominants from three separate regions, *Stipa*, *Agropyrum* and *Koeleria* coming from Holarctica, *Sporobolus* from the south, and the short-grasses from the Mexican plateaux, and it still exhibits the closest kinship with the Eurasian steppe. It contains nearly all the genera that serve as dominants in the related associations, while many of the eudominants of these have all the appearance of direct derivatives from its species, as is shown by *Stipa*, *Sporobolus*, *Poa*, and *Agropyrum*. The evolution of both species and communities is evidently in response to the various subclimates, that of the true prairie being moister, of the coastal warmer as well; the desert plains are hotter and drier, the California prairie marked by winter rainfall and the Palouse by snowfall.

*Consociation.*

In its typical form the consociation is constituted by a single dominant, but as a matter of convenience the term is also applied to cases in which other dominants are but sparingly present and hence have no real share in the control of the community. It has likewise been convenient to refer in the abstract to each major dominant of the association as a consociation, though with the realization that it occurs more frequently in mixture than by itself. In this sense it may be considered a unit of the association, though the actual area of the latter is to be regarded as divided into definite faciations. Consociation dominants fall into a more or less regular series with respect to factor requirements, especially water content, and often exhibit zonation in consequence. This is a general feature of mixed prairie where *Agropyrum smithi* and *Stipa comata* are the chief mid-grasses, the former occupying swales and lower slopes, the latter upper slopes and ridges.

The consociation achieves definite expression over a considerable area only when the factors concerned fluctuate within the limits set by the requirements of the dominant or when the other dominants are not found in the region. The first case may be illustrated by *Pinus ponderosa* in the lower part of the montane forest and by *Adenostoma fasciculatum* in the Sierran chaparral, while the second is exemplified by *Picea engelmanni* in the Front Range of Colorado, its usual associate, *Abies lasiocarpa*, being absent from the district. In rolling terrain like that of the prairie, each consociation will recur constantly in the proper situation but is necessarily fragmentary in nature. Such behavior is characteristic of dominants with a postclimax tendency, as with *Stipa minor* and *Elymus condensatus* in swales and lower levels of the mixed prairie.

*Faciation.*

This is the concrete subdivision of the association, the entire area of the latter being made up of the various faciations, except for seral stages or fragments of the several consociations. Each faciation corresponds to a particular regional climate of real but smaller differences in rainfall/evaporation and temperature. It may be characterized by one or two eudominants, such as *Hilaria jamesi* and *Stipa pennata* in the southern mixed prairie, but more often it derives its individuality from a sorting out or a recombination of the dominants of the association. As is evident, the term is formed from the stem *fac-*, show, appear, as seen in *face* and *facies*, and the suffix *-ation*, which denotes a climax unit.

During the past decade, much attention has been given to the recognition and limitation of faciations on the basis of the presence or absence of a eudominant, such as *Hilaria*, *Buchloe*, or *Carex*, or a change in the rank or grouping of common dominants, like *Stipa*, *Agropyrum*, *Sporobolus* or *Bouteloua*. In the prairie this task has been complicated by overgrazing, cultivation and related disturbances, while selective lumbering and fire have added to the

difficulties, in the deciduous forest especially. In general, temperature appears to play the leading part in the differentiation of faciations, since they usually fall into a sequence determined by latitude or altitude, though rainfall/evaporation is naturally concerned also. The mixed prairie exhibits the largest number, but it is approached in this respect by the deciduous forest as a consequence of wide extent and numerous dominants. Over the Great Plains from north to south, the successive faciations are *Stipa-Bouteloua*, *Bouteloua-Carex*, *Stipa-Agropyrum-Buchloe*, *Bouteloua-Buchloe*, *Hilaria-Stipa-Bouteloua*, and *Agropyrum-Bouteloua*. However, the short-grass communities are to be regarded as disclimaxes wherever the mid-grasses have been eliminated or nearly so, a condition that fluctuates in relation to dry and wet phases of the climatic cycle.

#### *Lociation.*

In its turn, the lociation is the subdivision of the faciation, the term being derived from *locus*, place, as indicating a general locality rather than a large region. Nevertheless, a lociation may occupy a relatively extensive territory up to a hundred miles or more in extent, by comparison with several hundred for the faciation. It is characterized by more or less local differences in the abundance and grouping of two or more dominants of the faciation. These correspond to considerable variations in soil, contour, slope-exposure or altitude, but all within the limits of the faciation concerned. As a consequence, lociations are very often fragmented, recurring here and there as alternates with each other, and frequently with proclimaxes of various types. Like most climax units, they have been modified by disturbance in some degree, and this fact must be constantly kept in mind in the task of distinguishing them from subclimax or disclimax.

A detailed knowledge of the faciation is prerequisite to the recognition of the various lociations in it. The number for a particular faciation naturally depends upon the extent of the latter and the number of dominants concerned. Consequently, lociations are more numerous in the faciations of the mixed prairie and desert plains, of the chaparral and the oak-hickory forest. As would be expected, they are often most distinct in ecotones and in districts where there is local intrusion of another dominant. In correspondence with their local character, it is important to eliminate or diminish superimposed differences through restoration of the original cover by means of protection enclosures and thus render it possible to disclose the true composition.

#### *Society.*

This term has had a wide range of application, but by dynamic ecologists it has generally been employed for various groupings of subdominants, of which those constituted by aspects or by layers are the most important. In addition, there is a host of minor communities formed by cryptogams in the ground layer or on host-plants and other matrices. The soil itself represents a



major layer, divisible into more or less definite sublayers. Animals regularly assume roles of varying importance in all of these, especially the insects, arachnids and crustacea, and hence most if not all societies comprise both subdominant plants and subinfluent animals. It is doubtful whether animals form true societies independently of their food-plants or those used for materials or shelter, but this is a question that can be answered only after the simplest units, namely, family and colony, have been recognized and coordinated in terms of their coactions.

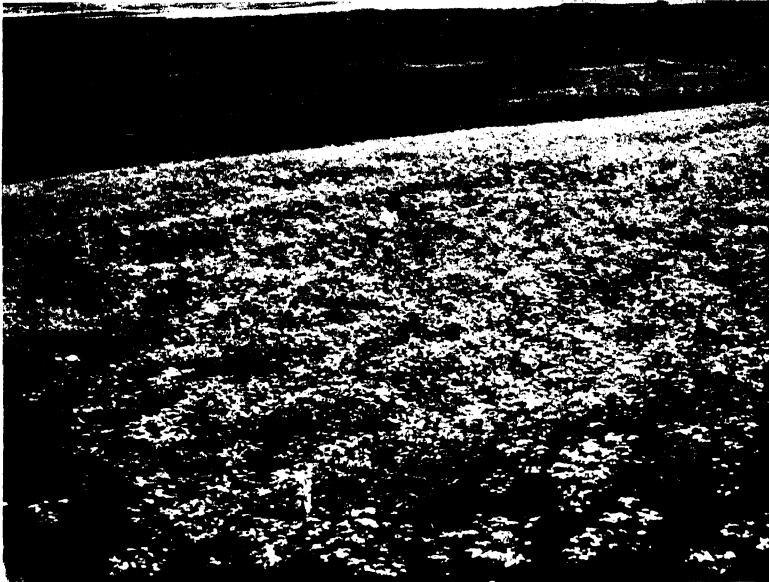
In view of what has been said previously, it seems desirable to employ society as the general term for all communities of subdominants and sub-influents above the rank of family and colony, much as community is the inclusive term for all groupings of whatsoever rank. This then permits carrying out the suggestion made two decades ago that the major types of societies be set apart by distinctive names. In accordance, it is here proposed to call the aspect society a *sociation* and the layer society a *lamiation*, while the corresponding seral terms would be *sociés* and *lamies*. Many of the societies of cryptogams and minute animals would find their place in these, particularly so for those of the surface and soil layers, but many others take part in a miniature sere or *serule*, such as that of a moldering log, and may best receive designations that suggest this relation.

*Sociation.* Wherever societies are well developed, they regularly manifest a fairly definite seasonal sequence, producing what have long been known as aspects (Pound and Clements, 1898). As phenomena of the growing season, these were first distinguished as early spring or prevernal, vernal proper, estival, and serotinal or autumnal, but there may also be a hiemal aspect, especially for animals, in correspondence with an actual and not merely a calendar winter as in California.

Sociations are determined primarily by the relation between the life cycle of the subdominants and the seasonal march of direct factors, temperature in particular. So far as the matrix of plants is concerned, the constituent species may be in evidence throughout the season, but they give character to it only during the period of flowering, or fruiting in the case of cryptogams. They are present largely or wholly by sufferance of the dominants, and they are to be related to the reactions of these and competition among themselves rather more than to the habitat factors as such. In grassland and desert, they are often more striking than the dominants themselves, sometimes owing to stature but chiefly as an effect of color and abundance, and they may also attain much prominence in woods with the canopy not too dense.

Sociations are usually most conspicuous and best developed in grassland, four or even five distinct aspects occurring in the true prairie from early spring to autumn. In the mixed prairie these are usually reduced to three, and in the desert plains and desert proper, to two major ones, summer and winter, in which however there may be subaspects marked by *sations*, as indicated





Phot. 11. Sociation of *Erigeron* and *Psoralea*, estival aspect; Belmont Prairie, Lincoln, Nebraska.



Phot. 12. Lamination of mid-herbs, *Laportea*, *Physostegia*, *Impatiens*, etc., in Oak-Hickory forest.

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later. Short seasons due to increasing latitude or altitude afford less opportunity, and the tundra, both alpine and arctic, usually exhibits but two aspects, the sociations however taking a conspicuous role as in the prairie. In woodland the number and character of the sociations depend largely upon the nature of the canopy, and for deciduous forest the flowery sociations regularly belong to the spring and autumn aspects, when the foliage is either developing or disappearing.

It is convenient to distinguish sociations as simple or mixed with respect to the plant matrix in accordance with the presence of a single subdominant or of two or more. However, when animals are included in the grouping, such a distinction appears misleading and may well be dropped. The word "mixed" would be more properly applied to plant-animal societies were it not for the fact that this appears to be the universal condition. Since seasonal insects are legion, many of the societies in which they take part are best denoted as sations.

*Lamination.* The term for a layer society is derived from the stem *lam-*, seen in lamina and lamella. As is well known, layers are best developed in forests with a canopy of medium density, so that under the most favorable conditions as many as five or six may be recognized above the soil. In such instances, there are usually two shrub stories, an upper and lower, often much interrupted, followed by tall, medium and low forb layers, and a ground community of mosses, lichens and other fungi, and usually some delicate annuals (cf. Hult, 1881; Grevillius, 1894). The soil population is perhaps best treated as a single unit, though it may exhibit more or less definite sublayers. When the various layers beneath the dominants are distinct, each is regarded as a lamiation, but in many cases only one or two are sufficiently organized to warrant designation, e.g. shrub or tall-herb lamiation.

Layers are often reduced to a single lamiation of low herbs in the climax forest, especially of conifers, and even this may be entirely lacking in dense chaparral. Two or three layers of forbs may be present in true prairie in particular, the upper lamiation being much the most definite and often concealing the grass dominants in the estival aspect, but the structure of grassland generally reflects the greater importance of sociations. Climaxes of sagebrush and desert scrub exhibit no proper lamiations, owing to the interval between the individual dominants, but the herbaceous societies of the interspaces show something of this nature.

As a rule, well-developed lamiations also manifest a seasonal rhythm, corresponding to aspects or to subaspects. These constitute recognizable groupings in the lamiation and for the sake of determination and analysis may be termed *sations*. This word is a doublet of season, both being derived from the root *sa-*, sow, hence grow or appear. Because of the frequent interplay of aspects and layers, the sation may for the present be employed for the subdivision of both sociation and lamiation, and especially where seasonal species of invertebrates play a conspicuous role.

*Clan.* This is a small community of subordinate importance but commonly of distinctive character. It is marked by a density that excludes all or nearly all competing species, in consequence of types of propagation that agree in the possession of short offshoots. Extension is usually by bulb, corm, tuber, stolon or short rootstock, each of which produces a more or less definite family grouping; in fact, most clans are families developed in the climax matrix and sometimes with a blurred outline in consequence. Clans of a particular species such as *Delphinium azureum* or *Solidago mollis* are dotted throughout the respective sociation, often in large numbers, and contribute a distinctive impress much beyond their abundance. Like all units, but small ones especially, they are subject to much fluctuation with the climatic cycle, as a result of which they may pass into societies or be formed by the shrinkage of the latter.

#### *Seral units.*

The concepts of dominance and subdominance apply to the sere as they do to the climax, as does that of influence also, and the corresponding sets of units bear the same general relation to each other. Each of the four major units is the developmental equivalent of a similar community in the climax series and this is likewise true of the various kinds of societies. They constitute the successive stages of each sere, both primary and secondary, including the subclimax, where they often achieve their best expression. It has also been customary to employ seral terms for preclimax and postclimax, and this appears to be the better usage for disclimax and proclimaxes in general. From the fragmentary nature of bare areas and suitable water bodies in particular, seral communities are often but partially developed and one or more units will be lacking in consequence. Thus, the reed-swamp associates is frequently represented by a single one of its several consociates and the minor units are even more commonly absent.

The associates is the major unit of every sere, the number being relatively large in the prisere and small in the subere. The universal and best understood examples are those of the hydrosere, in which *Lemna*, *Potamogeton*, *Nuphar*, *Nymphaea*, *Nelumbo* and others form the consociates of the floating stage, and *Scirpus*, *Typha*, *Phragmites*, etc., are the dominants of the reed-swamp or amphibious associates. As already indicated, every consociate may occur singly and often does when the habitat offers just the proper conditions for it or the others have failed to reach the particular spot. When the ecial range is wider, various combinations of two or three dominants will appear, to constitute corresponding facies. Locies are less definitely marked as a rule, except in swamps of vast extent, but are to be recognized by the abundance of reed-like dominants of lower stature, belonging to other species of *Scirpus*, to *Heleocharis*, *Juncus*, etc. Both facies and locies seem to be better developed in sedge-swamp with its larger number of dominants, though the Everglades with the single consociates of *Cladium* form a striking exception.

The tree-swamps of the south-eastern United States contain a considerable number of consocieties, such as *Taxodium distichum*, *Nyssa aquatica*, *biflora* and *ogeche*, *Carya aquatica*, *Planera aquatica*, *Persea palustris* and *borbonia*, *Magnolia virginiana*, *Fraxinus pauciflora*, *profunda* and *caroliniana*, and *Quercus nigra*. These are variously combined in several different facies, though a more detailed and exact study of the swamp sere may show the presence of two woody associates, distinguished by the depth or duration of the water. As with other scrub communities, the heath associates of peat-bog and muskeag comprises a large number of dominants and presents a corresponding wealth of facies and locies.

In the hydrosere of the deciduous forest, the typical subclimax is that of the flood-plain associates, composed of species of *Quercus*, *Ulmus*, *Fraxinus*, *Acer*, *Betula*, *Juglans*, *Celtis*, *Platanus*, *Liquidambar*, *Populus* and *Salix* for the most part. There are at least three well-marked facies, namely, northern, central and southern, each with a number of more or less distinct locies. The swamp associates or subclimax of the lake and boreal forests consists of *Larix laricina*, *Picea mariana* and *Thuja occidentalis*, occurring often as consocieties but generally in the form of zoned facies. A large number of fire subclimaxes appear in the form of consocieties, as with many of the pines, but associates are frequent along the Atlantic Coast, as they are in the boreal climax, where aspens and birches are chiefly concerned. The number of shrubs and small trees that play the part of seral dominants in the deciduous climax is much larger, producing not merely a wide range of associates but of facies and locies as well. More than a dozen genera and a score or so of species are involved, chief among them being *Sassafras*, *Diospyrus*, *Asimina*, *Hamamelis*, *Prunus*, *Ilex*, *Crataegus* and *Robinia*. The subclimax of the xerosere is constituted for the most part by species of *Quercus*, forming an eastern, a south-eastern and a western associates, the last with two well-marked facies, one of *stellata* and *marilandica*, the other of *macrocarpa* and *Carya ovata*.

Among postclimax associates, those of grassland and scrub possess a large number of dominants and exhibit a corresponding variety of facies and locies, together with fairly definite consocieties. In the sandhills of Nebraska, the tall-grasses concerned are *Andropogon halli*, *furcatus* and *nutans*, *Calamovilfa longifolia*, *Eragrostis trichodes*, *Elymus canadensis* and *Panicum virgatum*; some of these drop out to the northward and others to the south, thus producing at least three regional facies. The mesquite-acacia associates of the south-west possesses a larger number of dominants and manifests a greater variety of facies through its wide area, and this is likewise true of the coastal sagebrush of California.

With reference to seral societies, it must suffice to point out that these are of necessity poorly developed in the initial stages of both hydrosere and xerosere, as the dominants are relatively few. Even in the reed-swamp, true layers are the exception, being largely restricted to such subdominants as

*Alisma*, *Pontederia*, *Hydrocotyle* and *Sagittaria*, which are found mostly in borders and intervals. However, in extensive subclimaxes and postclimaxes the situation is quite different. The tall-grass associates of sandhills is often quite as rich in saties and lamies as the true prairie, while the various subclimaxes of the several great forest types may equal the latter in the wealth of subdominants for each season and layer, the actual communities being very much the same.

### *Serule.*

This term, a diminutive of *sere*, has been employed for a great variety of miniature successions that run their short but somewhat complex course within the control of a major community, especially the climax and subclimax. They resemble ordinary seres in arising in bare spots or on matrices of different sorts, such as earth, duff, litter, rocks, logs, cadavers, etc. Parasites and saprophytes play a prominent and often exclusive role in them, and plants and animals may alternate in the dominant parts. The organisms range from microscopic bacteria and worms to mites, larvae and imagoes on the one hand and large fleshy and shelf fungi on the other. The most important of these in terms of coaction and abundance are known as *dominules* (Clements and Shelford, 1936), with *subdominule* and *edominule* as terms for the two degrees of lesser importance. On the same model are formed *associiule*, *consociiule*, and *sociiule* in general correspondence with the units of the sere itself. In addition there are families and colonies of these minute organisms, which are essentially similar to those of the initial stages of the major succession. Up to the present, little attention has been devoted to the development and structure of serules, but they are coming to receive adequate consideration in connection with bio-ecological problems. Many of the coactions, however, have long been the subject of detailed research in the conversion of organic materials.

### RANK AND CORRESPONDENCE OF UNITS

The following table exhibits the actual units of climax and sere, as well as their correspondence with each other. However, for the complete and accurate analysis of a great climax and especially the continental mass of vegetation, it is necessary to invoke other concepts, chiefly that of the proclimax and of communities mixed in space or in time. The several proclimaxes have been characterized (pp. 262-8), and the ecocline and seration briefly defined (p. 267). To these are to be added the *ecotone* and *micrium*, both terms of long standing, the former applied to the mixing of dominants between two units, the latter to the mixed community that intervenes between two seral stages or associates. Finally, there will be the several types of seres in all possible stages of development, the prisere in the form of hydrosere, xerosere, halosere or psammosere in regions less disturbed and a myriad of subseres in those long settled.

## TABLE OF CLIMAX AND SERAL UNITS

<i>Climax</i>	Eoclimax Panclimax	<i>Sere</i>
	Climax (formation)	
Association		Associes
Consociation		Consocieties
Faciation		Facies
Lociation		Locies
Sociation		Societies
Lamiation		Lamies
Sation		Saties
Clan		Colony
	<i>Serule</i>	Family
	Associule	
	Consociule	
	Sociule	

As indicated previously, the word *community* is employed as a general term to designate any or all of the preceding units, while *society* may well be used to include those of the second division, i.e. sociation, etc. These are characterized by subdominants in contrast to the dominants that mark the first group. It has also been pointed out that the entire area of the association is divided into faciations and that the consociation is the relatively local expression of complete or nearly complete dominance on the part of a single species. The clan corresponds to the family as a rule, but in some cases resembles the colony in being formed by two species.

Families and colonies may also appear in climax communities, but this is regularly in connection with the serule.

*Panclimax and eoclimax*

The comprehensive treatment of these concepts is reserved for the succeeding paper in the present series, but it is desirable to characterize them meanwhile. The *panclimax* ( $\pi\alpha\nu$ , all, whole) comprises the two or more related climaxes or formations of the same general climatic features, the same life-form and common genera of dominants. The relationship is regarded as due to their origin from an ancestral climax or *eoclimax* ( $\eta\acute{o}\varsigma$ , dawn), of Tertiary or even earlier time, as a consequence of continental emergence and climatic differentiation. In the past, eoclimaxes formed a series of great biotic zones in the northern hemisphere with the pole as a focus, and this zonal disposition or clisere is still largely evident in the arrangement of panclimaxes at the present. It is striking in the case of the arctic tundra and taiga or boreal forest, fairly evident for deciduous forest and prairie-steppe, and somewhat obscure for woodland and chaparral-macchia, while the position of deserts is largely determined by intervening mountain ranges. This is true likewise of grassland in some degree, and taken with the former broad land connection between North and South America explains why both prairie and desert panclimax contain at least one austral formation.



In the light of what has been said earlier, it is readily understood that panclimax and panformation are exact synonyms, as are eoclimax and eoformation. Panbiome and eobiome are the corresponding terms when the biotic community is taken as the basis for research.

*Prerequisites to research in climaxes*

It would be entirely superfluous to state that the major difficulty in the analysis of vegetation is its complexity, were it not for the fact that it is too often taken as the warrant for the static viewpoint. This was embodied in the original idea of the formation as a unit in which communities were assembled on a physiognomic basis, quite irrespective of generic composition and phyletic relationship. It is not strange that this view and its corollaries should have persisted long past its period of usefulness, since this is exactly what happened with the artificial system of Linnaeus, but the time has come to recognize fully that a natural system of communities must be built just as certainly upon development and consequent relationship as must that of plant families. Complexity is an argument for this rather than against it, and especially in view of the fact that the complexity discloses a definite pattern when the touchstone of development is applied to it.

Though the mosaic of vegetation may appear to be a veritable kaleidoscope in countries long occupied by man, the changes wrought upon it are readily intelligible in terms of the processes concerned. As emphasized previously, the primary control is that of climate, in a descending scale of units that correspond to formation, association, and faciation. Upon this general pattern are wrought the more circumscribed effects of physiography and soil, and both climatic and edaphic figures are overlaid and often more or less completely obscured with a veneer applied by disturbance of all possible kinds. Even above this may be discerned the effect, transient but nonetheless apparent, of such recurrent changes as annuation and aspection. Moreover, the orderly pattern of climate is complicated by great mountain ranges so that such climaxes as tundra and taiga occur far beyond their proper zone, and the effect is further varied by the relative position of the axis.

The migrations of climaxes in the past are a prolific source of fragmentary relicts, the interpretation of which is impossible except in terms of dynamics. This is likewise true of savannah, which represents the shrinkage of forest and scrub under a drying climate and is then usually further modified by fire or grazing. Fragmentation from this and other causes is characteristic of every diversified terrain and reaches its maximum when human utilization enters the scene upon a large scale. Somewhat similar in effect though not in process is the reduction of number of dominants by distance, with the consequence that an association of several may be converted into a consociation of one. Such a shrinkage naturally bears some relation also to climate and physiography, especially as seen in the glacial period, and finds its best illustration in the

general poverty of dominants in the coniferous and deciduous climaxes of Europe, by contrast with those of eastern Asia and North America. A similar contrast obtains between the grassland of Asia and of North America, the latter being much richer in dominants, while South America approximates it closely in this respect.

On the part of the investigator, the difficulties in the way of an extensive and thoroughgoing study of climaxes are usually more serious. They arise partly from the handicap too often set by state or national boundaries and partly from the limitations of funds and time. They are also not unrelated to the fact that it is easiest to know a small district well and to assume that it reflects larger ones with much fidelity. As a consequence, it is impossible to lay too much stress upon the need for combining intensive and extensive methods in the research upon climaxes, insofar as their nature, limits and structure are concerned. The detailed development in terms of primary and secondary succession lends itself much more readily to local or regional investigation, but even here a wider perspective is essential to accurate generalization.

## REFERENCES

- Bradbury, J.** "Travels in the Interior of North America, ca. 1815." In **Thwaites' Early Western Travels**, 5, 1904.
- Bromley, S. W.** "The original forest types of southern New England." *Ecol. Mon.* 5, 61-89, 1935.
- Chaney, R. W.** "A comparative study of the Bridge Creek flora and the modern redwood forest." *Publ. Carneg. Instn.* No. 349, 1925.
- Chaney, R. W. and E. I. Sanborn.** "The Goshen Flora of West-central Oregon." *Publ. Carneg. Instn.* No. 439, 1933.
- Chapman, H. H.** "Is the longleaf type a climax?" *Ecology*, 13, 328-34, 1932.
- Clements, F. E.** *Plant Physiology and Ecology*, New York, 1907.
- Clements, F. E.** *Plant Succession*, Washington, 1916.
- Clements, F. E.** "Development and structure of the biome." *Ecol. Soc. Abs.* 1916.
- Clements, F. E.** *Plant Indicators*, Washington, 1920.
- Clements, F. E.** "Phylogeny and classification of climaxes." *Yearb. Carneg. Instn.* 24, 334-5, 1925.
- Clements, F. E.** *Plant Succession and Indicators*, New York, 1928.
- Clements, F. E.** "The relict method in dynamic ecology." *This JOURN.* 22, 39-68, 1934.
- Clements, F. E.** "Origin of the desert climate and climax in North America." *This JOURN.* 24, 1936.
- Clements, F. E. and E. S. Clements.** "Climate and climax." *Yearb. Carneg. Instn.* 32, 203, 1933.
- Clements, F. E. and V. E. Shelford.** *Bio-ecology*, 1936.
- Du Rietz, G. E.** "Classification and nomenclature of vegetation." *Svensk. Bot. Tid.* 24, 489, 1930.
- Godwin, H.** "The subclimax and deflected succession." *This JOURN.* 17, 144, 1929.
- Greely, H.** *An Overland Journey to California in 1859*, New York, 1860.
- Greivillius, A. Y.** "Biologisch-physiologische Untersuchungen einiger Schwedischen Hainthälchen." *Bot. Z.* 52, 147-68, 1894.
- Hult, R.** "Försök til analytisk behandling af växformationerna." *Medd. Soc. Faun. Flor. Fenn.* 8, 1881.
- Hult, R.** "Blekinges vegetation. Ett bidrag till växformationernas utvecklingshistorie." *Medd. Soc. Faun. Flor. Fenn.* 12, 161, 1885. *Bot. Zbl.* 27, 192, 1888.
- Lewis, M. and W. Clark.** Journal, 1803-1806. In **Thwaites' The Original Journals of the Lewis and Clark Expedition**, 1904-05.
- Phillips, J.** "The biotic community." *This JOURN.* 19, 1-24, 1931.

- Phillips, J.** "Succession, development, the climax and the complex organism: an analysis of concepts. Part I." *This JOURNAL*, **22**, 554-71, 1934.
- Phillips, J.** "Succession, development, the climax and the complex organism: an analysis of concepts. Part II." *This JOURNAL*, **23**, 210-46, 1935.
- Phillips, J.** "Succession, development, the climax and the complex organism: an analysis of concepts. Part III." *This JOURNAL*, **23**, 488-508, 1935.
- Rübel, E.** *Pflanzengesellschaften der Erde*, Bern-Berlin, 1930.
- Sargent, C. S.** *Report on the Forests of North America (exclusive of Mexico)*, Washington, 1884.
- Seton, E. T.** *Lives of Game Animals*, **3**, New York, 1929.
- Shelford, V. E.** "Basic principles of the classification of communities and habitats and the use of terms." *Ecology*, **13**, 105-20, 1932.
- Short, C. W.** "Observations on the botany of Illinois." *West. J. Med. Surg.* **3**, 185, 1845.
- Tansley, A. G.** "Editorial note." *This JOURNAL*, **17**, 146-7, 1929.
- Tansley, A. G.** "The use and abuse of vegetational concepts and terms." *Ecology*, **16**, 284-307, 1935.
- Tournefort, J. P.** *Relation d'un Voyage du Levant*, Paris, 1717.
- Weaver, J. E. and F. E. Clements.** *Plant Ecology*, New York, 1929.
- Weaver, J. E. and E. L. Flory.** "Stability of climax prairie and some environmental changes resulting from breaking." *Ecology*, **15**, 333-47, 1934.

# CONCEPTS AND CRITERIA FOR THE RECOGNITION OF COMMUNITIES

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THE concepts of the association have undergone a marked metamorphosis during the past two decades. The earlier controversies over the criteria for community recognition—whether physiognomy or biotic composition was to be the deciding factor—have been largely settled with the ascendant concepts of succession and climax. It is the purpose of this paper to set forth the concepts underlying the present usages of the ecological units set forth by Clements and Shelford and now used by many American and British authors. For full definitions of the several terms to be discussed as they have appeared in the ecological literature from time to time the reader is referred to “A glossary of terms used in ecology and related sciences” (in press) by the author.

## I. THE CONCEPTS OF THE ABSTRACT AND CONCRETE COMMUNITY

### (a) *The “association abstract”*

In more recent years it has been agreed by the majority of the workers that to be treated as a definite community a biotic population should be reasonably uniform in composition as to dominants and predominants throughout its range. It is not at all unusual that this range is found to be interrupted frequently by such local and edaphic characters as those determined by hill slopes, rock outcrops, stream valleys, and the like. In spite of the fact that a community may be so intersected at intervals by other communities, it nevertheless retains its integrity and is recognised as a biotic entity. For example, the continuity of the grassland associations of North America is in no wise questioned because they are traversed by rivers and streams, in spite of the fact that in many cases the entire physiognomy and growth form as well as the species change entirely in the local regions.

### (b) *The concept of the “abstract community” and relict communities*

This concept has received a more liberal application in the consideration of *relict* communities (see Clements, 1934). Invasion by a successor often results in small isolated stands of a former widespread community which are known as relicts. The interstices between the stands may be very large, but the dominants and physiognomy common to all bind them together and give the scattered whole the status of a single entity. Individually each of the stands of climax rank are termed “associations” and are the “associations concrete” of authors. The general type to which the individual stands or concrete associations con-

form has been termed the "association abstract" or the "association type" (see Nichols, 1918, p. 275, 1923, p. 13).

(c) *The concept of the "associes abstract"*

Personal observation as well as the observations of others has shown that many seral stages over a large area often conform to a given type which may well be termed the *associes abstract* or *associes type*. For example, certain seral stages in the river flood-plain succession in north-eastern Minnesota studied by George-Barclay (1924) bear a very close resemblance to those of the south Canadian river flood-plain in central and western Oklahoma studied by Hefley (1935). This resemblance is more than superficial, since the floristic composition, the physiognomy, and the influence exerted by the community on the habitat are essentially similar. It should be noted that in spite of the similarity of the seral stages the climaxes are, in this instance, different. Other instances might be cited of seres leading to similar climaxes or the same climax. In either case, dominants and subdominants (and frequently predominant and influents as well) lend sufficient similarity to certain, often widely, geographically separated seral stages (*associes*) to bring them together in the concept of the abstract *associes type*.

(d) *The concept of abstract grouping and the "formies"*

Similar communities require essentially similar habitats which are brought about in seral succession by essentially similar processes. It is not surprising therefore that seres over a large area include several *associes* in sequence, each displaying the similarity cited above. These stands (*Bestände*) of a given community may occupy different positions with reference to the climax in their respective individual seres in different localities. Hence a concept of seral succession up to the turning point in the sere toward the climax may be formulated which embodies the consideration together of similar portions of like seres over a given area. The term applied to this abstract grouping is the *formies* (Shelford, 1932, p. 111) which is a grouping (or "formation") of developmental communities rather than a formation in its developmental stages as the term has on occasion been interpreted. Thus the *formies* is a grouping of developmental stages as the *formation* is a grouping of climax communities.

## II. THE SUBDIVISIONS OF THE BIOTIC FORMATION (BIOME)

The nomenclature of the community units of lesser rank within the *biotic formation* (sense of Clements and Shelford) has been modified and added to from time to time, and in some cases the criteria for the recognition of these units have not perhaps been made fully clear. The communities will here be taken up according to their period of duration, namely, annual, seasonal, and

diel.<sup>1</sup> A conspectus of the discussion may be obtained from the accompanying table.

Table I. *The subdivisions of the biotic formation (biome)*

Duration	Climax units	Dominants*	Sub-dominants*	Pre-dominants* major influents	Sub-influents* minor influents	Seral units
Perennial nucleus	Association complex		×	×	×	Locality-complex¶
	Association†	<i>a, b, c</i>				Associates†
	Presociation			×		Pre-associates‡
						Pre-associates complexes‡
	Faciation†	<i>a, b, c, + d</i> <i>a, b, - d</i>				Facies†
	Consociation†	<i>a</i>				Consociates†
Seasonal	Lociation		×			Locies
	Society§		×		×	Societies§
	Presociety§				×	Presocieties§
Diel	Phase			×	×	Phase

\* See footnote 2 below.

† Distribution of dominant species (plants on land) (*a, b, c*) may result in one dominant (*c*) dropping out, thus causing a faciation (composed of *a* and *b*) to be recognised, or all save one may drop out leaving a "pure stand" or consociation (of *a*). A faciation may also be formed by the addition of another dominant (*d*) (thus forming a faciation of *a, b, c, + d*).

‡ Only rarely will predominants, etc., be restricted to a single seral stage; hence the designations of pioneer (or initial), midseral, and subclimax pre-associates complexes of seral stages may be applied.

§ Classed as *prevernal, vernal, estival, serotinal, autumnal* and *hiemal* or *hibernal*.

|| Classed as *auroral, diurnal, vespereal* and *nocturnal*.

¶ The *locality complex* may be considered as including both the climax and seral stages of a given region bound together by ranging influents and predominants.

### (a) *The perennial nucleus*

Communities of association (or associates) rank are usually designated by workers adhering to the American and British schools of ecology by the *dominant* components of the *perennial nucleus*, i.e. the dominant members of the community which are present throughout the entire year. To illustrate and characterise communities of associational rank let us take an association which is characterised by three dominants<sup>2</sup> which may be designated as *a, b*, and *c*. The local addition or loss of a dominant (*a, b, c + d*, or *a, b - c*) results in the presence of a *faciation* (*facies*<sup>3</sup>). A pure stand (from the standpoint of dominance, at least) of a single dominant of the original association is considered as a *consociation* (*consociates*<sup>3</sup>); here all save one dominant have dropped out (and the composition is therefore *a - b, c*). If all of the dominants drop out or re-

<sup>1</sup> The term *Diel* is used in the sense of the day of 24 hours, as distinguished from the *Diurnal* or sunlit portion of the day (Carpenter, 1935, p. 209).

<sup>2</sup> Plants are usually considered as the dominants on land, while the dominants of fresh water and marine aquatic communities are usually animals. Predominants and influents are animals on land (see Newcombe, 1935, p. 235).

<sup>3</sup> The developmental equivalent of the climax unit.

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main in subordinate position and are replaced as dominants by other species, of course a new association is to be recognised.

Within an association, differences in the subdominant forms only result in a *lociation* (*locies*<sup>1</sup>); here there is no appreciable change in the composition of the dominants as such. If the predominants or (perennial) major influent forms change but the dominants do not, a *presociation* is recognised (see Woodbury, 1933, p. 168). Strictly speaking, the *pre-associates* is the developmental equivalent here. However, predominants and other animals are but rarely restricted to a single seral stage, and the designation of *pioneer* or *initial*, *midseral*, and *subclimax pre-associates complexes of seral stages* may be applied to groups of seral stages bound together by ranging influents and predominants. In local areas and particularly along ecotone margins between two associations many species are found not to be restricted to a single community but rather to range throughout the general area, thus binding the locality together into a complex of several associations or an *association complex*. Since in many instances these forms range throughout both climax and subclimax areas they are seldom restricted in fact to subclimax areas alone, the *locality complex* may be distinguished. This latter is equivalent in many instances to the "environmental complex" of authors.

### (b) *Seasonal societies (societies<sup>1</sup>) of communities*

The seasonal stages in aspection<sup>2</sup> result in the formation of seasonal *societies (societies<sup>1</sup>)* which are recognised by the presence of *seasonal subdominants and subinfluents*.<sup>3</sup> The term *presociety* was originally used in the sense of an "animal society of an animal community" (Shackleford, 1929; Smith-Davidson, 1928). Since community ecology is essentially "bio-ecology" the term *presocieties* must be restricted to instances where the animal forms react differently to the seasonal microclimate than do the plants. An example here is that of certain forms in a community undergoing hibernation during the hiemal season while others remain active during the same period (see Carpenter, 1935, p. 207). Hence hiemal and hibernal societies (*societies<sup>1</sup>*) may be recognised during the winter while consistent behaviour of the biota results in but one society during the other seasons, namely the *prevernal*, *vernal*, *estival*, *serotinal*, and *autumnal* societies.

### (c) "*Intradiel*" subcommunities

Mass movements on the part of animal populations on land and of plankton in water as well as variations in the physiological activity of all organisms in all environments during the several periods of the 24-hour day constitute the diel<sup>4</sup>

<sup>1</sup> The developmental equivalent of the climax unit.

<sup>2</sup> Formerly termed "seasonal succession"; this change precludes confusion with seral succession.

<sup>3</sup> See p. 287, footnote 2.

<sup>4</sup> The term *Diel* is used in the sense of the day of 24 hours, as distinguished from the *Diurnal* or sunlit portion of the day (Carpenter, 1935, p. 209).

fluctuations of communities. The periods of the day have been designated as *Phases* of the seasonal society to which they belong. *Auroral, diurnal, vespereal*, and *nocturnal* phases have been recognised for the several periods of the day (Carpenter, 1935).

Table I summarises the second portion of this discussion. The criteria for recognising the type of community within the formation are indicated by (×) with the exceptions explained at the foot of the table.

## REFERENCES

- Carpenter, J. R. "Fluctuations in biotic communities. I. Prairie-forest ecotone of central Illinois." *Ecology*, **16**, No. 2, pp. 203-12, 1935.
- Carpenter, J. R. *A glossary of terms used in ecology and related sciences*. Univ. of Oklahoma Press: Norman (in press).
- Clements, F. E. "The development and structure of vegetation." *Rep. Bot. Survey of Nebraska*, **7**, 1904.
- Clements, F. E. "Plant succession." *Publ. Carneg. Instn*, No. 242, 1916.
- Clements, F. E. "The relict method in dynamic ecology." *This JOURN.* **22**, No. 1, pp. 39-68, 1934.
- Clements, F. E. and Shelford, V. E. "Concepts and objectives in bioecology." *Yearb. Carneg. Instn*, **26**, 335, 1927.
- Cooper, W. S. "The fundamentals of vegetational change." *Ecology*, **7**, No. 4, pp. 392-413, 1926.
- Du Rietz, G. E. "Vegetationsforschung auf soziationsanalytischer Grundlage." *Handb. biol. Arbeitsmeth.* 1930.
- Gleason, H. A. "The structure and development of the plant association." *Bull. Torrey Bot. Cl.* **43**, 463-81, 1917.
- Gleason, H. A. "The individualistic concept of the plant association." *Bull. Torrey Bot. Cl.* **53**, 7-23, 1926.
- George-Barclay, H. "The plant succession of the flood-plain of the Mississippi river with special reference to the pioneer stage." Thesis, Univ. of Minnesota Library (unpublished), 1924.
- Hefley, H. M. "Ecological studies on the South Canadian river flood-plain in Cleveland county, Oklahoma." Thesis, Univ. of Oklahoma Library (unpublished), 1935.
- Newcombe, C. L. "A study of the community relationships of the sea mussel, *Mytilus edulis* L." *Ecology*, **16**, No. 2, pp. 234-43, 1935.
- Nichols, G. E. "The interpretation and application of certain terms and concepts in the ecological classification of communities." *Plant World*, **20**, 305-19, 341-53, 1917.
- Nichols, G. E. "The vegetation of Northern Cape Breton Island, Nova Scotia." *Trans. Conn. Acad. Arts and Sci.* **22**, pp. 249-467.
- Nichols, G. E. "A working basis for the ecological classification of plant communities." *Ecology*, **4**, No. 1, pp. 11-23, No. 2, pp. 154-77, 1923.
- Nichols, G. E. "Plant associations and their classifications." *Proc. Intern. Congress Plant Sciences*, pp. 629-41, 1929.
- Phillips, J. "The biotic community." *This JOURN.* **19**, No. 1, pp. 1-24, 1931.
- Phillips, J. "Succession, development, the climax, and the climax organism: an analysis of concepts." Part I: *This JOURN.* **22**, No. 2, pp. 554-71, 1934. Part II: *This JOURN.* **23**, No. 1, pp. 210-46, 1935. Part III: *This JOURN.* **23**, No. 2, pp. 488-508, 1935.
- Shackleford, M. W. "Animal communities of an Illinois prairie." *Ecology*, **10**, No. 1, pp. 126-54, 1929.
- Shelford, V. E. "Terms and concepts in animal ecology." *Ecology*, **7**, No. 3, p. 389, 1926.
- Shelford, V. E. "Some concepts of bioecology." *Ecology*, **12**, No. 3, pp. 455-67, 1931.
- Shelford, V. E. "Basic principles on the classification of communities and habitats and the use of terms." *Ecology*, **13**, No. 2, pp. 105-20, 1932.
- Smith-Davidson, V. G. "Animal communities of the deciduous forest succession." *Ecology*, **9**, No. 4, pp. 479-500, 1928.
- Tansley, A. G. "The classification of vegetation and the concept of development." *This JOURN.* **8**, No. 2, pp. 118-44, 1920.
- Woodbury, A. M. "Biotic relationships of Zion canyon, Utah, with special reference to succession." *Ecological Monographs*, **3**, 148-245, 1933.



## REVIEWS

### THE JOURNAL OF ANIMAL ECOLOGY

(VOL. 4, NO. 2, NOVEMBER, 1935)

THIS number has thirteen original papers, one note, reviews, and 119 notices of British publications on animal ecology. There are three general ecological surveys. F. Loxham Kidd, K. A. Pyefinch, and P. M. Butler carried out a preliminary reconnaissance of Bardsey Island in North Wales. John Ford investigated the soil fauna of a pasture near Oxford and found several hundred million animals per acre, of which over 90 per cent. were springtails (Collembola). 132 species of animals from soil and surface vegetation are listed. H. P. Moon, also using quantitative sampling methods, studied the influence of changing levels of the water on the littoral fauna of Lake Windermere. K. R. Allen worked out the relation of perch to the plankton of the same lake, and found that the size of food taken changed as the fish grew larger, through a series of small to larger plankton, to bottom fauna, and finally to fish. These changes are partly associated also with migration. The marked powers of survival of small invertebrates and plants from a pool above high water mark were shown experimentally by James H. Fraser: two surveys of parasites are described. James W. Campbell collected gapeworms (two species of *Syngamus*) from a large number of wild birds. Especially high infestation was found in young rooks. Gordon B. Thompson records the first results of an ectoparasite census of ducks and geese in Uganda, collected by G. H. E. Hopkins and other members of the agricultural laboratories in that country. The distribution of East African bird life in various land habitats is discussed in an extensive paper by R. E. Moreau, who concludes that existing theories about the factors limiting habitat occupation are inadequate. He believes that subjective factors may be important in the birds' choice of habitat. Fluctuations in animal populations occupy four papers. H. F. Barnes concludes his important series of census studies at Rothamsted of insects and their parasites, with an account of the leaf-curling pear-midge (*Dasyneura pyri*), and a general review of his earlier papers. The recovery in numbers and continued spread of the grey squirrel in Great Britain are recorded by A. D. Middleton, who gives a detailed map of its distribution in 1935. Research on an epidemic among voles on the Scottish Border in the spring of 1934 was carried out by Charles Elton, D. H. S. Davis, and G. M. Findlay, who were enabled by forecasting the epidemic to study it thoroughly by means of field censuses and pathological experiments. In relation to this work, T. Russell Goddard made a census of short-eared owls during and after the epidemic, and found only one pair on about 2000 acres of plantation.

There is a note by A. D. Middleton on the stomach contents of a badger. Reviews deal with the August number of *The Journal of Ecology*, the micro-climates of a coffee plantation, Cambridgeshire bird life, recent mathematical and experimental studies on animal populations, a text-book of limnology, fishery research on the herring and the hake, and with North Atlantic bird life. The notices of publications on animal ecology, issued in duplicate form, for use on index cards, are now printed on gummed paper. They can be purchased separately for 3s. 6d. per year (two sets).

CHARLES ELTON.

**Schröter, C.** *Flora des Südens d.h. "Insubriens" des südlichen Tessins und Graubündens und des Gebietes der oberitalienischen Seen.* Pp. viii + 151, with 72 plates (32 coloured) and 59 text-figures. Zürich: Verlag Rascher. 1936. Price M. 9.50.

The latest of Prof. Schröter's attractive books (a little large for any but a capacious pocket) with coloured pictures of flowers and plants deals with that favoured region at the

southern foot of the Alps where the winters are milder than in most of North Italy, but the summers are less arid and have a much higher rainfall than those of the Mediterranean climate proper. The result is that the vegetation, both native and exotic, is extremely rich and varied, and the shores of the great Italian lakes are famous for their beautiful parks and gardens, in which a wide range of Mediterranean and subtropical species are cultivated. The native vegetation is not dominated by sclerophylls, but by deciduous trees and shrubs, mostly Central or Western European species, though a number of real Mediterranean plants are present, and others belonging to the most various "geographical" and "genetic" elements. These include a number of endemics, particularly in the hills to the east of the Lake of Como.

After a short description of the climatic factors and rock types, followed by an enumeration of the various elements of which the flora is composed and some account of how they arrived in the region, there is a description of the plants which may be found in various well-known localities for botanical excursions, and also descriptions with figures of interesting and beautiful groups such as the native orchids, the spring flora, water plants, etc., all illustrated by plates (nearly half of which are coloured) of the most conspicuous and interesting species.

A. G. T.

## TWO STUDIES OF SWISS FENS

**Zobrist, Leo.** Pflanzensoziologische und bodenkundliche Untersuchung des Schoenetum nigricantis im nordost-schweizerischen Mittellande. *Beitr. z. geobot. Landesaufnahme der Schweiz*, **18**. Pp. 144, with 37 figures including many photographs. Bern 16: Verlag Hans Huber. Price (Swiss) francs 9.50.

On its own lines this is a very thorough study of the succession of plant communities in several similar areas of what we in England should call *fen* situated in north-eastern Switzerland. The main area lies on a flat impermeable substratum left by a ground moraine, on which a lake was formed and lake marl deposited: above this comes the peat formed by the vegetation of the fen. The three main phases of the sere are dominated respectively by *Mariscus serratus* (*Cladium mariscus*), *Schoenus nigricans* and *S. ferrugineus*, and *Molinia caerulea*.

The *Mariscetum serrati* is a very pure community with few associated species, the most characteristic probably *Carex elata* and *C. lasiocarpa*. *Phragmites* occurs throughout, but not vigorous, and *Nymphaea alba* is pretty common as a relict of an earlier phase. The consociates often grows in shallow water and will not tolerate any degree of desiccation. The pH value of the surface peat varies from 7 to 7.7, with a mean and a mode of 7.4, and the calcium carbonate content is very high.

Next to the *Mariscetum* comes the *Schoenetum nigricantis*, first with abundance of *Eleocharis pauciflora* and the soil level still frequently below the summer water-level, then in typical development with *Schoenus ferrugineus* and hybrids and many abundant species. Though not necessarily at all abundant or constant the following are said to be "characteristic": *Orchis paluster*, *Gentiana utriculosa*, *Pinguicula vulgaris*, *Primula farinosa* and *Tofieldia calyculata*. The range of pH values is even higher than that in the *Mariscetum*, sometimes reaching 8.1, and the water is again rich in calcium carbonate, which is often deposited. The typical *Schoenetum nigricantis* passes over into a phase in which the plants are packed more closely and *Schoenus ferrugineus* is dominant. More numerous species appear, including *Molinia* as a constant associate, *Serratula tinctoria*, *Lysimachia vulgaris*,

*Gentiana pneumonanthe*, *Filipendula ulmaria*, *Angelica silvestris* and *Inula salicina*. The pH values here vary from 6·7 to 7·8, the mean content of carbonate of lime decreases and the humus increases. Though the peat is still thoroughly wet, water no longer stands above the surface.

Finally we come to the Molinietum caeruleae which is also separable into three phases, the wettest with *Carex hostiana*, then the typical form of the consociates with *C. panicea* and finally the driest with *C. tomentosa*. The Molinietum has about the same pH range but the various values are much more widely dispersed and there is a very much lower lime content. The ground water only reaches the surface in spring, while in summer there is considerable superficial drying. With the drier conditions disintegration of the peat has begun and also leaching. Many species are present which are not in the least characteristic of wet soils and the Molinietum is said to pass over in succession to dry meadow of the type of Mesobrometum erecti.

The Schoenetum has a certain value for "litter" but is only occasionally mowed. The Molinietum on the other hand is regularly cut and it is hard to find an example unaffected by mowing. In this way the succession to *Frangula-Salix cinerea* carr, whose further development would lead to Alnetum glutinosae, is prevented.

Zobrist's results on the acid and base buffering of the soils of the different seral communities, tending to keep the soil reaction constant in each habitat, are very interesting. He finds that the buffering against acids, fundamentally due to the calcium bicarbonate dissolved in the waters is strongest in the Mariscetum, remains high in the Schoenetum and falls off in the Molinietum. With increase in humus the buffering against bases rises, is at its maximum in the Schoenetum ferruginei, and falls off slightly in the Molinietum, but there exceeds the buffering against acids.

The strong resemblance between the Swiss fens described by Zobrist and the East Anglian fens is very striking. Both have or may have a stage of Mariscetum following reedswamp, and both show a Molinietum in a later phase, though *Schoenus* does not form a stage in the East Anglian succession. Both develop a fen scrub or carr in which *Salix cinerea* and *Frangula alnus* are dominant species, and there is evidence in Norfolk that Alnetum glutinosae is or may be a fen climax. The waters of both are highly calcareous and the pH values range between 7 and 8. Though the Swiss fens are much richer in species, a considerable number of the accompanying plants are identical.

In the British Isles *Schoenus nigricans* occurs locally in calcareous fens and marshes through much of the country. But in the west it also occurs in non-calcareous bogs, in association with *Trichophorum caespitosum* (*Scirpus caespitosus*) and is locally dominant. Zobrist mentions an association of *Schoenus ferrugineus* and the *Trichophorum* in the subalpine zone of Switzerland and Savoy. The peat of the western Irish bogs in which *Schoenus nigricans* is dominant is extremely acid, so that the species is far from being an obligate basiphil throughout its range.

A. G. T.

**Lüdi, W.** Das Grosse Moos in westschweizerischen Seelände und die Geschichte seiner Entstehung. *Veröffentl. des Geobot. Institutes Rübel in Zürich*, 11. Pp. 344, with 2 maps, 3 profile plates and 47 other illustrations. Bern: 1935, Hans Huber.

This is not an analysis of existing vegetation but a very careful and detailed account of the history of the great peat area, now drained and cultivated, west of Solothurn, between the Bielersee and the Neuenburgersee (Lake of Neuchâtel). On the retreat of one of the big Alpine glaciers at the end of the Pleistocene ice age a great lake 100 km. long was held up in this region by the terminal moraine of the glacier. Large parts of the lake were

in course of time filled up by detritus brought down by streams flowing into the lake from the neighbouring Jura on the north and by the Aar on the south, so that the original lake was divided into fragments, now represented by the Bielersee, Murtensee and Neuenburgersee. The level of the water, however, underwent many fluctuations, described in detail by the author, apparently partly owing to corresponding changes of climate, partly to damming of the outlet by the carrying down of detritus or erosion of the detrital dams, and to changes in the course of the Aar. In all, five major inundations have been recognised. When the water level rose deposits of sand, loam and lake marl spread over the bottom, the soil level being then gradually raised by the growth of vegetation and the formation of peat on the top of the mineral deposits. When the "moss" was at its driest it was colonised by trees—alder, willow, pine and eventually oak, silver fir, a little beech, and finally spruce. The maximal colonisation by trees apparently took place during the Bronze Age. Later there was another great inundation with great increase of alder and decrease or disappearance of other trees, and the lake level remained relatively high from Roman times throughout the Middle Ages. Finally between 1868 and 1880 the region was thoroughly drained by diverting and canalising the Aar and by cutting drainage ditches, so that the water level in the lakes was lowered by more than 2 metres and the area brought under cultivation. The vegetation of the "moss" was dominated by reedswamp and fen plants. The work is well illustrated by charts, soil profiles, pollen diagrams and photographs.

A. G. T.

#### THE SEVENTH (ITALIAN) I.P.E.

**Rübel, E.** (redigiert von). *Ergebnisse der Internationalen Pflanzengeographischen Excursion durch Mittelitalien, 1934. Veröffentl. d. Geobot. Institutes Rübel in Zürich*, 12. Pp. 239. Bern 16: Verlag Hans Huber. 1935.

Dr Rübel, who has taken the leading part in securing the perpetuation and proper organisation of the triennial (or sometimes biennial) International Phytogeographical Excursions, does good service by editing these "Results" of successive expeditions and arranging for their publication through the Institute which he founded in Zürich some years ago. A captious critic might perhaps complain that the volumes are less "results" of the successive excursions than contributions by the members on any phytogeographical topics on which they may feel able to write, by preference related to the region in which the excursion was made. But even so these collections of papers by expert phytogeographers are very useful. Of the strictly topical papers in the present volume Dr Lüdi contributes a new attempt to separate the vegetational (climatic) regions of Italy, or rather, as he calls it, of the Apennine Peninsula, excluding the wide extension north, east and west of North Italy into the main continental mass. In his map (p. 235) the four following "formations" or "climax regions" are distinguished, starting from the coast and proceeding towards the Apennines: *Quercion ilicis*, *Quercion pubescentis*, *Fagion silvaticae*, and Alpine Vegetation. Of these the first (the Mediterranean vegetation in the strict sense) occupies only a belt, of varying width and for the most part very narrow, round the coast, the second the greater part of the peninsula, and the third substantial areas on the mountains. The small part played by conifers in the mountain forests of Italy is well known. Dr Gams contributes a learned, very well documented paper in which he deals with the factors determining the limits and classification of the evergreen Mediterranean vegetation. This brings out very clearly how extremely complex the problems are and how inadequate are the data at present available for their solution.

A paper which is a genuine "result" of the Excursion is a short contribution by Dr Rytz of Bern on the Oreophyte flora of the Apuan Alps—the north-western mountains which

include the famous quarries of Carrara and extend southwards to the Serchio valley. Here are found a number of endemics together with a number of species widely separated from the nearest area of their occurrence. They are "oreophytes" inhabiting, not the highest peaks, but the middle ranges of the mountains and have nothing in common with the Apennine oreophyte flora, which are mostly "eu-oreophytes", i.e. species whose nearest allies are also oreophytes. Rytz compares the Apuan florula (which mostly consists of "hemi-oreophytes", i.e. species whose nearest allies are "pediophytes" or species of the plains) with a similar collection of species found on the Pienine Mountains in southern Poland (visited by the Fifth I.P.E. in 1928), which is equally distinct from the oreophytic flora of the neighbouring Carpathians. In both cases the author attributes the origin of these local florulae of hemi-oreophytes to the uplifting of the particular range which they inhabit. Both Pienines and Apuan Alps are much older than Carpathians and Apennines. The presence of the eu-oreophytes on the latter are attributed to wholesale migrations resulting from such widespread changes of climate as were brought about by the Pleistocene glaciations and their retreats: of the hemi-oreophytes on the former to the effect of local mountain building.

Dr Firbas and Dr Zangheri contribute a short paper on a glacial flora from Forli, south of Ravenna: Dr Negri, the leader, a diary of the Excursion; and the Editor a report of the permanent committee of the Excursions. Dr Wangerin publishes a long general paper on phytogeographical analysis and characterisation of plant communities, with special reference to beechwoods.

A. G. T.

## SOIL SCIENCE

*Transactions of the Third International Congress of Soil Science, Oxford, 1935.*

Vol. I. Commission Papers. Pp. x+428. Price 28s. Vol. II. Plenary Session Papers and the Presidential Address. Pp. 194. Price 13s. London: Thomas Murby and Co., 1, Fleet Lane, E.C. 4.

The Third International Congress of Soil Science held at Oxford at the end of July and the beginning of August, 1935, under the Presidency of Sir John Russell, was, by common consent, a very great success. More than 400 people, from nearly every country, attended, and were loud in their praises, alike of the interest of the meetings, of the beauty of Oxford, and of the superb summer weather. The Congress was the best possible evidence, if evidence were now needed, of the contemporary vigour and wide range of this comparatively young branch of science.

The report of the Congress is an exceedingly useful collection of papers, the greater portion (included in vol. I) prepared and issued before the Congress as a basis for discussion in the six "commissions", between which the work of the International Society of Soil Science is divided, the remainder (vol. II) being those which were read at the plenary sessions of the whole Congress: a third volume of supplementary papers is still to appear. It is obviously impossible here to notice a tithe of the 170 papers printed, and it would be invidious to make an arbitrary selection where so many are of first-rate quality. It must therefore suffice to say that considerably more than half the papers are of interest, and a large number of great importance, to plant ecologists, whose subject is so closely bound up with soil science that it is impossible to dissociate them.

## THE HEAT ECONOMY OF PLANTS

**Huber, Bruno.** "Der Wärmehaushalt der Pflanzen." *Naturwissenschaft und Landwirtschaft*. Heft 17. Pp. 148, with 37 figures and many tables. Freising bei München: F. P. Datterer and Co. 1935. Price M. 5-60.

The author points out the effect of the early conclusion that plants were "poikilothermic", following the temperatures of their environment, in diverting interest from the actual temperatures of the plant body. Askenasy made an early observation that even in Central Europe succulents might reach temperatures of more than 50° C., while Schimper mentioned 60-70° C. in the tropics and subtropics—temperatures much higher than those of the surrounding air. This is sufficient to show that real problems are involved in the capacity of some plant cells to withstand temperatures far above the usual thermal death points (45-55° C.). On the physical side of the problem Brown and Escombe's study of the energy interchanges between foliage leaves and their environment laid firm foundations, and within the last few years many new observations of plant temperatures have accumulated. Huber holds that plants may even be said to regulate their temperatures, to some extent, at least, by the structure and position of their organs and by such physiological processes as transpiration and respiration, so that we may properly speak of the heat economy, just as of the water economy, of plants.

The main source of high temperatures in plant tissues (apart from the highly specialised inhabitants of hot springs and the neighbourhood of volcanoes) is of course insolation, and the cooling factor is principally the loss of heat in transpiration. The quantitative relations of these two factors are carefully described by Huber, who shows, among other things, that the smaller or the more finely divided the leaves the more closely they follow the surrounding air temperature. Such leaves are well-known to be prevalent in sclerophyll vegetation where the danger of over-heating is great, the surface of the soil often reaching very high temperatures. Here, indeed, Huber thinks, the "heat economy" of the plant takes precedence over the "water economy". The massive succulents, of course, form a biological class apart. Often living in habitats exposed to very strong insolation, their tissues possess a whole series of special characteristics, among which is the ability to endure high temperatures.

In the last section of his work the author raises the question of the biological significance of the temperatures of plant organs, and it is this of course that directly concerns the ecologist. Primarily the study of the effects of comparatively small changes of temperature in parts or organs of plants is in no way involved with teleology—the observation for example that the growth of a peach is increased, while that of an apple is diminished, on the side turned towards the sun—it is simple description of fact. But the enquiry, what would be the result if the temperature of an organ were a few degrees higher or lower than it actually is under given conditions, whether perhaps quite small changes of temperature may be important, or even decisive, for the existence of a species, is certainly of first-rate ecological significance. The author shows that very small variations of temperature near the upper thermal death-point may be enough to determine the life or death of a plant, organ or tissue, and that such temperatures occur pretty frequently even in Central Europe, not to mention the Mediterranean region and subtropical deserts. Heat killing in fact is quite common. Massive organs such as thick stems and fruits are more susceptible to such injury than thin organs like leaves, because of the lowering of temperature through transpiration. And all sorts of conditions in the living cell itself—many of which are very little understood—affect its susceptibility to heat. Our knowledge of the whole subject is still too little developed to enable any extensive and trustworthy ecological conclusions to be

drawn. It is still difficult in many cases to distinguish between the effects of excessive heat, excessive light, and deficiency of water. But it is certain that there is a specific and variable quality of heat-resistance just as there is of drought resistance in the living cells.

The effects of extreme cold, since they raise quite separate problems, are deliberately omitted from this work.

A. G. T.

## THE ALGAE

**Tilden, Josephine, E.** *The Algae and their life relations: Fundamentals of Phycology.* Pp. xii + 550, with a coloured frontispiece and 257 figures in the text. Minneapolis and London: Univ. of Minnesota Press; Oxford Univ. Press (Humphrey Milford). 1935. Price \$5, English price 22s. 6d.

Prof. Tilden, of the University of Minnesota, well known as a leading American phycolist, has written a book remarkable for many valuable and original features. The greater portion is devoted to a systematic treatment of the different phyla, orders, families, and genera, but the introductory and concluding chapters deal with problems interesting to the ecologist. Adopting the modern theory of independent evolution of the great phyla of Algae separated by the pigments they contain, the author holds that they appeared in terrestrial waters in the following order: Myxophyceae (Cyanophyceae), Rhodophyceae, Phaeophyceae, Chrysophyceae, Chlorophyceae. Degree of illumination, she holds, was the great determining factor. The Myxophyceae were the primitive forms, characteristic of the ages when weak light alone reached the surface of the earth and general temperatures were still high. As the light intensity gradually increased the different cell pigments characteristic of the various phyla became successively dominant in the algal cell, culminating in the pure green of the Chlorophyceae, inhabiting the upper littoral zones of the sea and the freshwaters of the land surface. The Myxophyceae meanwhile persisted and spread, enabled to endure the stronger light through the protection afforded by their thick gelatinous sheaths, and at the same time to enjoy the high temperatures of tropical and thermal waters.

In concluding chapters Prof. Tilden deals with algal control, the algal food of animals, and the desirability of using marine algae as accessory food stuffs for man. She discusses the poisoning of inland waters by the Myxophycean "water blooms", insists on the importance of seaweeds in the food of fish and lays stress on the immense significance of the algae as a source of vitamins. In all these fields she pleads for more extended, and more intensive research into the life histories, distribution, ecology and physiology of algae.

A. G. T.

## THE DESTRUCTIVENESS OF THE HUMAN ANIMAL

**Sears, Paul B.** *Deserts on the March.* Norman, Oklahoma: University of Oklahoma Press. Pp. 231. 1935. Price \$2.50.

The title of Prof. Sears' first chapter—"Man, maker of Wilderness"—gives the key to the burden of his book. He writes in fluent and non-technical language not devoid of distinction, and he tells the depressing story of man's careless wastefulness in dealing with the resources of nature on which perforce he must live, and of its tragic consequences. He begins with the Old World and sketches the history of those regions which have long supported a dense population—China proper, India and the Nile delta. Even in China, where the inhabitants have successfully established and maintained their life and culture through very many centuries, the author shows that they may justly be accused of living on borrowed capital—the capital of natural resources—which is not replaced at a rate commensurate

with the expenditure. When he turns to the United States we get the same process, but with the tempo immensely increased. Within three centuries, quite slowly at first, but with fearful rapidity during the last hundred years, man has ravaged the entire subcontinent, felling forest, overgrazing and ploughing up prairie, the maintenance of which was essential to his permanent welfare. General decrease in fertility, soil erosion on a huge scale, and extensive flooding are the inevitable results, with widespread human misery as their sequel. There is no longer fresh virgin land to which the farmer can move, and the future is not too bright, despite extensive public assistance and what science can offer in the way of introducing a more rational scheme of agriculture. The author rejects the abolition of private property and the adoption of communism as appropriate remedies, but his positive suggestions are rather hesitating and do not seem very convincing. One of them is a scale of taxation adjusted so as to encourage good management of farms, another the appointment of an ecologist for every county, just as a city appoints a municipal chemist. And it is true enough that the ecological approach is vital to the proper utilisation of land. But who would take the ecologist's advice about the utilisation and treatment of land if he thought it conflicted with his immediate interests? More hopeful perhaps is improved education of the young, who may learn wisdom from contemplating the mistakes of their elders, if a better way is pointed out to them. The root of the matter seems to be the same in all the urgent social problems which to-day confront every so-called civilised community. Man's enormously increased technical knowledge and consequent power to interfere with natural processes have broken up the old stable equilibria of his community life in relation to its environment, and he is unable to construct new equilibria because of his want of foresight, and, it must be added, of his selfishness and greed. Science has given him the added powers and could tell him how they should be used, but will he listen? He is like a selfish and mischievous but vigorous child who has got hold of complicated and dangerous weapons or machinery. Morally he has never grown up, and his intellectual development is narrow and one-sided. Better education in the use of reason and foresight, as well as in the social sense, seems the only hope, for it is true that these things can be taught. The future seems to depend on a race between the universal application of systematic efforts in such directions and the forces which are making for the wholesale destruction of our civilisations.

A. G. T.

**Weaver, J. E. and Noll, W. C.** *Comparison of run-off and erosion in prairie, pasture, and cultivated land.* University of Nebraska. Contribution from the Department of Botany, No. 96. 1935. Pp. 37.

As a detailed illustration of Prof. Sears' general thesis this study is very much to the point. "Soil erosion resulting from run-off water has come to be recognised as a national menace" are the opening words of the author. "Fully 75 per cent. of the crop-producing and grazing areas of the United States is sloping enough to set in motion, moderately or violently, these wasteful processes of accelerated soil-removal and excessive run-off—35 million acres of formerly cultivated land have been essentially ruined by erosion and an additional area of about 125 million acres, still largely in cultivation, have lost all or most of the top soil, with another 100 million acres of cropland heading in the same direction" (Bennett, 1934).

Much has been written on the effect of a forest cover in promoting absorption of rainfall and preventing erosion: Messrs Weaver and Noll show the same for unbroken prairie. By means of specially constructed boxes, installed in excavations so that their upper edges were flush with the soil, at the bottom of a slope of 10° gradient, they have compared the run-off from unbroken, though mown prairie with 95 per cent. foliage cover (1), with closely



grazed prairie—50 per cent. cover (2), and also with a slope of practically bare ground resulting from continued close grazing during the dry summer of 1934, and supporting only a few blades of grass and annual weeds—no cover (3). The vegetation of the areas was kept closely cut during the experiment. Throughout the period run-off water from the prairie was clear, from the pasture often turbid and even muddy, from the bare ground “roily” and often carrying much sediment. The total run-off from the prairie only amounted to 2.5 per cent. of the total rainfall, and there was no measurable erosion; from the pasture 9.1 per cent. and a small amount of erosion; from the bare area 15.1 per cent. and 5.08 tons of soil per acre were washed away.

Other experiments were performed in which natural rainfall was imitated by watering from watering cans by several people together, so that any desired amount of water could be administered during a given period, the behaviour of the soil surface in relation to intake of water observed, and the time when run-off began and stopped after beginning and ending of the watering ascertained. In the prairie run-off began later, was smaller in amount and ceased sooner. This was due partly to the greater interference with the movement of water by the ungrazed vegetation, but perhaps chiefly to the greater porosity of the untrampled soil. In one experiment in which 2.5 in. of water were given in two periods in one day during a total time of 1½ hours the run-off from the prairie was nil, from the pasture 29.3 per cent. and from the bare area 50.4 per cent. Penetration into the soil 5 days after the watering was 42 in. in the prairie, 22 in. in the pasture and 19 in. in the bare area. This decreased penetration explains the failure of springs and streams in overgrazed and eroded areas. In another experiment erosion in the prairie was nil, in the pasture 355 lb. per acre, and in the bare area 4.67 tons per acre. Run-off and removal of soil were greatest at first when the soil surface was dry. Steepness of slope increases erosion on bare or partly bare soil, but not on soil with continuous grass cover.

Overgrazing is the main cause of the partial baring of the soil which results in excessive run-off and serious erosion. Through much of the western United States the amount of run-off is approximately proportional to the sparsity of plant cover, the loss of surface litter and the compacting of the soil; and the partial or complete loss of plant cover is most dangerous in areas of relatively low rainfall where conservation of the soil is the critical need. Overgrazing is probably responsible for much more abnormal erosion on unbroken land than all other causes combined.

Similar results were obtained in a comparison of prairie, stubble, and fallow, with a slope of only 5 per cent. The total run-off from the application of 5 in. of water was 3.1 per cent. in the prairie, 27.6 per cent. in the stubble and 23.2 per cent. in the fallow, while the soil removed was practically nil in the prairie, 1.29 tons per acre in the stubble and 1.75 tons in the fallow. Losses from fields of alfalfa are often much less than from those of other crops, but grass cover (apart from forest) is the best means of retaining the water that falls in the soil.

**Gorrie, R. Maclagan.** *The Use and Misuse of Land.* Oxford Forestry Memoirs, No. 19. Pp. 80, with photographs and figures. Oxford: Clarendon Press, 1935.

Mr Gorrie's pamphlet is another striking illustration of Prof. Sears' thesis, and the evidence is again drawn from the United States, where the author has recently travelled 17,500 miles to study the problems of soil erosion. Unlike Prof. Weaver, Mr Gorrie is a forester by profession, and his previous experience has been mainly in India, but he has found in America excellent and widespread examples of the misuse of land, which are applicable in all semi-arid countries, whether the climate is tropical, subtropical, or tem-

perate, and he is fully aware of the value of grassland in resisting erosion and of the destruction caused by overgrazing.

The headings of the chapters will give some idea of the scope of his work: Forestry as a factor in land management, Grazing and range management, Overgrazing as a primary cause of soil erosion, Value of vegetational cover in stream-flow control, Forestry as a factor in farm and village economy, Farm erosion and its control, Other examples of the misuse of land, Public and private control of land.

The author illustrates just the same widespread destructive processes that are dealt with by Prof. Sears and Prof. Weaver, calling conspicuous attention to the rapid silting up of reservoirs and the consequent ruin of irrigation schemes—the complement of the removal of the top soil by erosion from arable and grazing land. Mr Gorrie holds that there are many areas of “forest” in the arid and semi-arid tropics and subtropics which are incapable of producing commercial timber but of value for grazing, besides water conservation and game. He points out that the U.S. Federal Forest Service have had to undertake grazing research and range management for the last quarter of a century, and rightly urges that the problems of land utilisation cannot be successfully dealt with piecemeal. He suggests that “the proper agency for holding and developing land and preventing abuses is a small but representative public body with sound technical advice at its disposal and sufficient powers to enforce its decisions”. On such a body, one may fairly add, ecology must be adequately represented if a co-ordinated understanding of the different elements of the problem, without which no action should be taken, is to be reached. “Private ownership and the common use of ‘waste’ land have almost invariably overworked one use and neglected other possibilities, failing to develop the ‘multiple use’ principle which can best serve the community as a whole.” In other words, we can no longer afford to leave great areas of country in private ownership. The world is too small, and man’s tendency to destroy, and his facilities for rapidly destroying, his own future welfare are too highly developed.

A. G. T.

## SCHOOL GARDENS AND THE MAKING OF PLANT COMMUNITY HABITATS

**Clarke, Lilian J.** *Botany as an experimental science in laboratory and garden.*

Pp. xvi + 138, with 35 illustrations. London: Humphrey Milford. 1935.

Price 6s.

The late Dr Lilian Clarke’s pioneer work in the teaching of practical botany at the James Allen Girls’ School at Dulwich is well known to most school teachers. This posthumous book gives a simple and straightforward account of its history and nature, and is of fascinating interest. We call attention to it in these pages because the description of the making of a whole series of “habitats” adjacent to the school in which could be grown the native plants which naturally live in them may serve as an inspiring example and also furnish useful hints to those who are trying to teach ecology in schools. Miss Clarke’s indomitable energy and great force of character enabled her to obtain the money and support necessary for starting the habitats—which included ponds, heath, bog, sand dune, shingle beach, saltmarsh, and oakwood. It is not every teacher who will be so fortunate, but the simple record of how the thing was done and of the striking success attained may stimulate others to attempt something similar. And every successful effort of the kind is of great benefit, not only to teacher and pupils, who take the deepest interest in this kind of work, but also to the study of ecology itself.

A. G. T.

## BRITISH ECOLOGICAL SOCIETY

ANNUAL MEETING (UNIVERSITY OF READING)  
JANUARY 3RD-5TH, 1936

THE twenty-third annual meeting of the Society began on the afternoon of January 3, the President, Prof. MATTHEWS, in the Chair.

Mr H. BAKER gave an account of a three years' study of seasonal variation in pH values of the soils of Bagley Wood, near Oxford. The results mainly concerned analyses made over a period of three years upon four types of woodland soil overlying respectively plateau gravel, sand, clay and clay loam. In all the soils there was a marked change of acidity with depth; in the sands and clays the subsoil was less acid but there was a reversal of the normal gradient in the clay loams. The most striking feature of the results was, however, a very marked tendency to a seasonal periodicity in acidity, expressed as a late summer maximum and a winter or early spring minimum, the bottom soils having a marked lag in this rhythm as compared with the upper soils. Mr Baker showed that rainfall seemed to have a considerable effect on the seasonal curve, disturbing the regularity of the rhythm. In the discussion which followed Dr Godwin, Prof. Tansley, Dr Clapham, Prof. Matthews and Dr Turrill took part and the hope was strongly expressed that Mr Baker would extend his studies for a further period of years, especially since the weather of 1933 and 1934 was decidedly abnormal.

Mr Ross read a paper on the regeneration of tropical rain-forest at a site 100 miles east-north-east of Lagos in Southern Nigeria. The characters of the undisturbed rain-forest and of the clearings made by the natives for cultivation were illustrated by very beautiful photographs taken on the Cambridge Botanical Expedition to Nigeria. Mr Ross then gave a detailed account of investigations on the vegetational processes following abandonment of such clearings after four or five years' occupation. Vegetational analyses showed a rapid colonisation by (1) weeds of cultivated land, (2) plants peculiar to secondary forest, and (3) seedlings of primary forest trees. In the second class the most permanent species was *Musanga smithii* (Musaceae), which became an early dominant in the secondary colonisation, reaching a height of 40 ft. at 6 years, but dying out, presumably through senescence, at about 50 years, when it had reached a height of 70 or 80 ft. Mr Ross showed that in all probability primary forest was rapidly re-established as a result of this secondary succession. In the discussion which followed Mr Gilmour, Prof. Tansley, Mr Fishlock, Dr Godwin and Mr Milne-Redhead took part.

Mr WILKINS gave an account of investigations carried out under his direction on the ecology of the larger fungi in various types of woodland near Haslemere in Surrey. Over a period of several years oakwoods, beechwoods, grassland, open heath and *Calluna* heath had been examined, but the larger number of examples were concerned with the oak and beechwoods. It appeared from the examination of fourteen beechwoods and eleven oakwoods that there was a greater constancy in the fungal species in individual oakwoods than in individual beechwoods, that the species of high constancy were mostly common ones, and that only a very few were exclusive species. At the same time, the common species varied much in constancy in the two types of woodland. Thus, for example, *Mycena pelianthina* was chiefly in the beechwoods, *M. polygramma* was common in oak and not in beech, *M. pura* was found only in beechwoods, and *M. sanguinolenta* was common in both. In conclusion, Mr Wilkins discussed the best methods of estimating the fungal flora of woods and many of the questions which followed turned on this point. Prof. Matthews and

Prof. Tansley, Dr Somerville Hastings, Dr Burt Davy, Dr Clapham, Mr Baker and Dr Watson took part in the discussion which followed.

*Exhibits in the Department of Botany*

After tea in the University Common Room members visited the exhibits set out in the Botanical Department.

Dr WATSON showed a number of lichens taken from the bark of oaks in *Quercus sessiliflora* woods growing on carboniferous limestone at Killarney, including *Parmelia atlantica*, a species newly created by Degelius.

Dr INGOLD had set out a series of rare fungi found in the neighbourhood of Reading, and specimens of the orchid, *Epipogon aphyllum*, which is also found locally.

Dr R. W. BUTCHER showed a series of herbarium specimens of water buttercups grown under varying experimental conditions: these included forms of *Ranunculus pellatus* with elongate peduncles, which have hitherto been described as varieties.

Prof. HARRIS showed an exhibit illustrating the effect of adding large amounts of nutrient to algal cultures. This treatment caused the disappearance of nearly all animals and filamentous algae, but the Protococcales increased enormously and were represented by about twenty species, many quite uncommon in Britain.

Dr HUBBARD set out a series of microscopic and herbarium preparations to illustrate the contrast in structure between tropical and temperate grasses. Tropical savanna grasses are characterised by a chlorenchyma closely set round the vascular bundles, whilst in many temperate grasses the chlorenchyma is evenly distributed through the mesophyll. Dr HUBBARD demonstrated that this structural difference could be recognised in tropical grasses naturalised in the British Isles, such as species of *Cynodon*, *Panicum*, etc., and he illustrated the value of the character as a taxonomic criterion.

Mr BALLARD showed some extremely interesting specimens of various members of the Cyperaceae, Velloziaceae and Gramineae, which have evolved a curious pseudodendroid habit, apparently in association with a rocky habitat and a long rainless period. *Microdracoides squamosus*, a native of West Africa, was perhaps the most striking of these species. The vertical rhizome, clothed by descending roots, progressively dies from the base although the plant itself continues living at the apex of this dead column of tissue.

Mr ROSS showed a series of photographs taken on the Cambridge Botanical Expedition to Nigeria illustrating the structure of primary and secondary rain-forest.

Dr GODWIN set out a series of pollen analysis diagrams from the Fenland showing the appearance of the beech and hornbeam in greater or less amount in the upper peat layers from several sites. It appeared from these results that the beech was present in East Anglia in pre-Roman times and probably began to increase in numbers in the late Bronze Age.

Members and guests were entertained in the evening at a *soirée* held in Wantage Hall. About fifty members and guests were present.

The annual meeting was resumed on the morning of January 4 at 10 a.m., about fifty members being present. Apologies for absence were read from Dr Gurney, Mr Oldham and Dr Pearsall.

The minutes of the last general meeting were read and confirmed.

The following new members were elected: Miss Waloff, Miss Eyre, Mr Plomley, Mr Mohr and Mr Horne.

The Treasurer reported on the finances of the Society and presented provisional accounts and balance sheet. He announced a deficit on the year's working. Prof. Tansley proposed the adoption of the accounts subject to correction and audit and this was approved

unanimously. Dr Watson proposed that Messrs William Norman and Son be reappointed auditors to the Society for 1936. A very hearty vote of thanks to Mr Boyd Watt for his valuable services as Treasurer was moved by Prof. Tansley and carried *nem. con.* It was proposed from the Chair and adopted *nem. con.* that the yearly grant of £5 for the transplant experiments of the Society be renewed for 1936. The Honorary Secretary's report on the work of the past year was read and adopted.

*Hon. Secretary's Report for the year 1935*

The twenty-first annual meeting of the Society was held in the Department of Botany, University College, London, on Saturday, January 5, 1935. A *soirée* was given on the evening before the meeting, and a large number of exhibits was on view, for the most part illustrative of ecological work carried out by research students and staff of the Department. A large number of members and guests were present at the *soirée*, and the sincere thanks of the Society are given to Prof. Salisbury for having organised it and for having again given generous facilities for meeting in his Department.

After careful consideration by the Council it was decided to accept the kind invitation of Prof. Hardy and Mr D'Oyly Good to hold a summer meeting of the Society under their joint leadership at Hull. It was fixed for August 28-31, 1935, and a programme of wide interest was arranged and circulated to members. The notifications of intention to attend were, however, so few that the meeting had to be cancelled. It seems probable that a major cause of the failure was the very intensive programme of excursions and meetings available to British botanists during the summer: at the same time there was equally little response from animal ecologists although many features intended to be of special interest to them had been arranged. The Society owes thanks to Dr Hardy and Mr Good for the considerable trouble they spent, and regrets that it should have been to no purpose. The Council would welcome more guidance and support from members in the arrangement of the summer meetings.

On Saturday, October 19, a joint excursion with the British Mycological Society was held at Box Hill under the leadership of Mr J. Ramsbottom. It was well attended.

In the past year two numbers of vol. iv of *The Journal of Animal Ecology* have been published, appearing in May and November. They contained respectively 165 and 172 pages, a considerable advance in size on the earlier volumes. In all twenty-nine original papers were published, with nine plates, in addition to notes, notices and reviews. Notices of publications on Animal Ecology have been continued, and in this volume totalled 226 classified entries.

Since the last annual meeting there have been issued two numbers of vol. xxiii of *The Journal of Ecology*, appearing in February and August and containing respectively 264 and 289 pages, with thirty-eight plates. In this volume have been published twenty-two original papers, besides book reviews and notices.

Mr Marsden Jones and Dr Turrill report continued satisfactory progress with the Society's transplant experiments at Potterne.

Since the last annual meeting the membership of the Society has risen from 331 to 341: there have been twenty-three new members elected, and thirteen members have resigned or died. Of the present membership list, 188 members receive *The Journal of Ecology*, 101 *The Journal of Animal Ecology* alone, 49 receive both Journals, and 3 neither. These figures include elections made at the General Meeting.

The Secretary then asked for the advice of the meeting on the question of the time and place of the summer excursion for 1936, and outlined the chief features of two alternatives, namely the Lake District and south-western Ireland. After some discussion it appeared that there was a general feeling in favour of the Irish excursion.

# BRITISH ECOLOGICAL SOCIETY

## REVENUE ACCOUNT FOR YEAR ENDING 31ST DECEMBER, 1935

### Income

	£	s.	d.	£	s.	d.
Subscriptions received, including arrears ...	472	7	10			
Less Prepayments for 1936-9 ...	22	0	0			
Less Transferred to <i>Journal of Animal Ecology</i> (see below) ...	450	7	10			
Interest on Investments ...	177	12	6	272	15	4
Interest on Deposit Account ...	34	10	0			
<i>Journal of Ecology</i> —Sales, etc.: Current volume, xxii, 1935 ...	1	5	2	35	15	2
Back volumes and parts ...	461	0	8			
Index Volume, <i>Journal of Ecology</i> (vols. i-xx), Sales ...	27	14	4	488	15	0
<i>Journal of Animal Ecology</i> —Sales, etc.: Vol. iv, 1935: Subscriptions received ...	177	12	6	6	3	4
Sales ...	167	16	4			
Sales of reprints ...	40	5	6			
Vols. i-iii: Sales of back numbers ...	54	18	3	440	12	7
Balance, Deficit for the Year ...				1244	1	5
				96	12	6
				£1340	13	11

### Expenditure

	£	s.	d.	£	s.	d.
<i>Working Expenses</i> : Printing Circulars, etc. ...				2	0	6
Postages, etc. ...				8	4	11
Bank Charges ...				4	4	5
Clerical assistance (Secretary and Treasurer) ...				15	0	0
<i>Soirée Expenses</i> ...	25	9	10			
Audit Fee ...	7	2	4			
<i>Grants</i> : Freshwater Biological Association of the British Empire ...	3	3	0			
B.E.S. Transplant Experiments Fund ...	10	0	0			
<i>Journal of Ecology</i> , vol. xxiii (1935): Paper, Printing, Illustrations, etc. ...	5	0	0			
Binding ...	680	2	0			
Publishers' Commission ...	4	1	0			
Carriage and Postages, Insurance, etc. ...	72	15	6			
Copies bought in ...	46	0	5			
	23	8	0			
Index Volume, <i>Journal of Ecology</i> , vols. i-xx: Sundry Expenses ...	826	6	11			
<i>Journal of Ecology</i> , vol. iv (1935): Paper, Printing, Illustrations, etc. ...	1	4	2			
Publishers' Commission ...	404	13	11			
Carriage, Insurance, Advertising, etc. ...	36	17	6			
	20	16	3			
	462	7	8			
	£1340	13	11			

## BALANCE SHEET AT 31ST DECEMBER, 1935

### Liabilities

	£	s.	d.	£	s.	d.
Membership Subscriptions, prepaid for 1936, etc....				22	0	0
<i>Journal of Animal Ecology</i> , vol. iv, pt. 2: Printing Account due ...	187	1	10			
Less Sale of reprints ...	6	7	0			
Library Account ...				180	14	10
General Revenue Account—Balance of Funds: Balance at 31st December, 1934 ...	983	7	6	1	5	0
Less Deficit at 31st December, 1935 ...	96	12	6			
				886	15	0
				£1100	14	10

### Assets

	£	s.	d.	£	s.	d.
<i>Westminster Bank—Credit Balances</i> : Current Account ...				76	16	10
Deposit Account ...	100	0	0			
<i>Sundry Debtors</i> : Subscriptions due ...	173	16	10			
<i>Investments</i> : £700 34% War Loan at cost (Market value at 31st December, 1935, at 106, £742) ...	11	5	0			
£200 5% Conversion Loan at cost (Market value at 31st December, 1935, at 120, £240) ...	717	3	0			
	198	10	0			
	915	13	0			
	£1100	14	10			

NOTE. A further asset is the unsold stock of the *Journals* and Index Volume held for the Society by the Publishers.

Audited and found correct and as shown by the Account Books of the Society. The Bank Balances have been verified by Bank Certificates.  
(Signed) WM NORMAN & SONS,  
Chartered Accountants.

The Council proceeded to the election of officers and the following were elected.

*President:* DR W. H. PEARSALL.

*Vice-President:* PROF. E. J. SALISBURY, F.R.S.

*Hon. Editor Journal of Ecology:* PROF. A. G. TANSLEY, F.R.S.

*Hon. Editor Journal of Animal Ecology:* MR C. S. ELTON.

*Hon. Secretary:* DR H. GODWIN.

*Ordinary Members of Council:* (in place of MR E. PRICE EVANS and PROF. SALISBURY) PROF. A. C. HARDY, DR W. LEACH.

In the absence of the new President and Vice-President Prof. Matthews was asked to continue in the Chair.

The revised constitution and rules of the Society as circulated beforehand to members were then discussed and unanimously adopted subject to a minor alteration proposed by Dr Watson and accepted *nem. con.* (see pp. 306-8).

At the conclusion of the business meeting Prof. T. A. STEPHENSON gave an account of the ecology of the intertidal region of the South African coast with special reference to the habits of limpets. The coastal fauna and flora of the Cape differs very sharply on the eastern and western coasts on account of the warm Agulhas current on the one side and the South Atlantic up-welling of polar water on the other. One method of attack on the problems of faunal distribution consisted in the examination of the behaviour of eleven species of limpet (*Patella*). An extremely interesting account was given of the breeding, zonation, geographical distribution and habits of these animals, and it was evident that a very close relationship existed between their method of life and their position on the shore. A great deal of interest centred in the feeding habits of such species as *P. granularis*, which feeds in the dark when the waves have retreated, leaving its scar on the rock, and browsing some distance away, to return directly to the same scar again with the rising tide. The wandering habit was more marked in the forms occupying upper littoral zones. In one species, *P. cochlea*, a grazed fringe of the red alga *Gelidium* was constantly associated with each limpet and various suggestions were put forward to explain the association. A very long and interesting discussion followed in which Dr Clapham, Prof. Tansley, Prof. Matthews, Prof. Weiss, Dr Ashby, Dr Watson, Mr Price Evans, Dr Burt Davy and Dr Godwin took part.

Dr A. R. CLAPHAM gave a concise statement of his views on the use of quantitative data on the distribution of individual plants and their statistical treatment in the study of vegetation. In briefly adverting to the history of the subject he suggested that statistical methods had been employed to elucidate (a) the space relations of individuals of one species, or the relations of one species to another; (b) the changes in distribution of species with time; and (c) in the definition and diagnosis of plant communities. He suggested that the methods were likely to be of use for purposes (a) and (b) rather than for (c), and explained a method of determining the dispersion of members of a species and expressing it in terms of "relative variance":

$$\frac{V}{m} = \frac{S_1^n (x - m)^2}{(n - 1)_m}.$$

$V/m$  is greater than unity in cases of over-dispersion (i.e. aggregation in patches) and is less than unity in under-dispersion (i.e. spacing more even than random spacing). He gave examples to show that there is a substantial change in the relative variance of species at different stages of a plant succession, and discussed cases in which the application of this method should prove useful. Prof. Tansley and Mr Valentine asked questions of the speaker, and Dr Ashby then gave an account of an alternative method, developed with Mr Stevens, of discovering the degree of under- or over-dispersion of individual species. This was based on random casts of a grid containing sixteen or twenty-five equal squares,

and the scoring of the number of individuals and the number of empty squares found within the grid. He quoted examples from open *Salicornietum* on salt-marsh, from regenerating birchwood and from abandoned arable ground on chalk downs. He also concluded that there was no valid method at present available for using statistics in the classification of vegetation and agreed that these methods should be applied to the examination of the distribution of individual species. In the following discussion Dr Godwin, Dr Turner, Dr Clapham, Dr Butcher and Mr Ross took part.

The meeting was adjourned for lunch in the Common Room and was resumed in the afternoon.

Prof. ADAMSON gave an account of a new classification of South African vegetation types. He emphasised the dependence of the vegetation on climate which was itself much influenced by topography, causing in particular a very striking change in the rainfall from east to west. The South African forests are very limited in extent and are little studied: they are mainly evergreen and show a striking absence of dominants. Four types are distinguishable, the subtropical rain-forest of the eastern coast, a small-leaved forest (Knysna type) of the southern coast allied to the sclerophyll bush of the Cape and in which *Olea* and *Podocarpus* are abundant, a more deciduous type in Natal and the south-east of the Cape Province and evergreen forest on higher mountains in a region of very heavy rainfall and mostly at about 5000–6000 ft. The rest of the country he separated into sclerophyll bushland, semi-desert with a rainfall below 12 in. and open vegetation with no dominants, savanna, bush veldt and grassland. He suggested that the grassland is separable from savanna by the much greater temperature extremes, particularly by frost making tree growth impossible; and the semi-desert region was subdivided on a basis of these temperature fluctuations, those parts with the greatest extremes having an open vegetation with dry scrub, the intermediate having succulents of the *Mesembryanthemum* type and those where frost is absent having succulents of large size. In the discussion which followed Prof. Tansley, Dr Burt Davy and Dr Godwin took part.

Prof. TANSLEY gave an account of experiments suggested by himself and carried out by Mr Baker and Dr Clapham on the early growth of *Quercus robur* and *Q. sessiliflora*. After a brief account of the climatic and soil preferences of the mature trees as usually understood, Prof. Tansley described experiments in which seeds of both species were sown in pots containing woodland soils of acidity varying from pH 3.6 to 8. There was exactly similar germination in both species and the soils showed no differential effect, but *Q. robur* grew taller in all soils, and the height growth of both species was greater on the more acid soils. The two species differed in the earlier emergence and growth of primary root and shoot in *Q. sessiliflora*, in the greater rate of growth of *Q. robur* in later stages, in the earlier slowing off of height growth in *Q. sessiliflora* correlated with the earlier date at which leaves of this species reached full size. A second series of experiments involving waterlogging of pot cultures showed that *Q. robur* suffers more severely than *sessiliflora*, though both are severely affected by complete waterlogging.

In the very interesting discussion which followed Dr Watson, Dr Godwin, Dr Thomas, Mr Gilmour, Mr Ross, Prof. Matthews and Mr Baker took part.

The meeting closed with the proposal by Prof. Weiss on behalf of the Society of a very hearty vote of thanks to the University authorities for their kind hospitality in giving the use of the University buildings and of Wantage Hall to the Society for the meeting, and to Professor and Mrs Harris for the kindness they had shown in entertaining us. This was carried with acclamation.

#### *Excursion to Beech Woods*

Owing to the unfortunate absence through indisposition of both Dr Watt and Mr Harley the proposed excursion to the Beech Woods of the Chiltern Hills had to be abandoned and an alternative shorter excursion was arranged under the leadership of Prof. Harris and



Dr Somerville Hastings. The party first visited, in the neighbourhood of Peppard Common, a small area of acidic heath formed on gravel over chalk and bearing characteristic vegetation with *Ulex minor*, *U. europaeus*, *Calluna* and *Pteridium*. On the other side of the valley there was an extremely characteristic area of chalk scrub showing abundant tree invasion by beech, ash, oak, holly, yew and elm. The party then proceeded to the main objective of the excursion, namely beech woods growing on chalk or on drift overlying chalk. Over large parts the beech had been exploited by selective cutting at a diameter of 6-8 in., the wood being used for the local manufacture of chair legs and brush backs, etc. The beech reaches a height of 55-60 ft. and *Fraxinus* and *Quercus robur* occur frequently, especially in the areas where cutting has taken place. Ground vegetation is generally sparse, though *Corylus*, *Sambucus*, *Daphne laureola*, *Prunus cerasus* occur locally and *Ilex* is often extremely abundant, spreading by suckers forming large thickets. The holly appears to be subject to the severe attack of rodents, most probably rabbits. The Society is much indebted to Prof. Harris and Dr Somerville Hastings for having organised such a satisfactory excursion on the spur of the moment.

## THE BRITISH ECOLOGICAL SOCIETY

FOUNDED 1913

### CONSTITUTION AND RULES

(Revised formulation adopted by the Society on January 4th, 1936)

1. The object of the BRITISH ECOLOGICAL SOCIETY shall be to promote and foster the study of Ecology in its widest sense.

2. The Society shall consist of Ordinary Members, Hon. Members and Associates as defined in these rules.

3. Applicants for Membership of the Society shall be proposed by one Member (from personal knowledge) or by an Officer of the Society (not necessarily with personal knowledge) and seconded by one or more other Members. Such applications shall be made on a form to be supplied by the Hon. Secretary, and duly filled up and signed by the applicant.

Election shall take place either at a General Meeting or at other times by resolution of the Council. A majority of votes in favour shall result in the election of the applicant.

The Secretary may, however, be empowered by the Council to circulate the names of applicants for membership to members of Council by post, and if he receives no intimation of objection within one week, the applicant shall be deemed to be elected.

4. Subscriptions shall be payable in advance and shall be due on January 1st each year. The minimum Annual Subscription for Ordinary Membership shall be twenty-five shillings (25s.) and for Associate Membership seven shillings and sixpence (7s. 6d.). Members who pay a yearly subscription of 25s. shall have the right to receive post free **either** *The Journal of Ecology* **or** *The Journal of Animal Ecology*. An Annual Subscription of 45s. shall entitle Members to receive post free **both** of the Journals above named.

5. In addition to receiving one or both of the Journals of the Society, ordinary members shall have the following privileges:

- (a) To receive on application any other publications of the Society free or at a reduced rate, as the Council may from time to time determine.
- (b) To have the use on loan, under regulations, of any photographs or lantern slides in the Society's collections, and of books, maps and pamphlets in the Society's Library.
- (c) To vote in the election of Council and of Officers.
- (d) To be eligible for service on the Council and its Committees, or as Officers.

6. Associate Members shall have the right to attend Meetings and Excursions, to obtain through the Secretary such advice and assistance as the Society can afford, to have the use of photographs and the Library, but they shall not have the privileges of Ordinary Members indicated in 5 (c) and 5 (d).

7. Local Natural History Societies may at the discretion of the Council be allowed to subscribe to the Society not less than twenty-five shillings (25s.) per annum and shall thereby be entitled to receive a copy of **either** of the two Journals of the Society, or on payment of forty-five shillings (45s.) per annum, to receive **both** Journals of the Society. In either case they shall also be entitled (a) to such advice or assistance as the Society can afford, and (b) to send two delegates to the Society's Meetings, to have the same privileges as Associate Members as regards such Meetings.

8. The Society shall be governed by a Council of fifteen Members consisting of the Officers of the Society, namely, the President, two Vice-Presidents, the two Hon. Editors, the Hon. Secretary and the Hon. Treasurer, together with as many ordinary members of Council as may be needed to raise the total to fifteen.

Officers and ordinary members of Council shall be elected at the Annual Meeting of the Society.

9. Each ordinary member of Council shall be elected for a period of four years, at the end of which time he shall retire. He shall not be eligible for re-election until the Annual Meeting of the year following that of his retirement.

An ordinary member of Council when elected an Officer of the Society shall cease to be an ordinary Council Member: on expiry of office the retiring President, Hon. Secretary, Hon. Treasurer and Hon. Editors shall be eligible for immediate re-election as ordinary members of Council, and the retiring Vice-President shall complete his term of four years' service on the Council.

10. The President and the two Vice-Presidents shall be nominated from among the Members of Council. The two Hon. Editors and the Hon. Secretary shall retire at the end of each year but shall be eligible for immediate re-election.

11. The President of the Society shall hold office for two years, and it shall be his duty to deliver an address to the Society at the Annual Meeting next after that at which he was elected.

12. One Vice-President shall be appointed each year and shall hold office for two years.

13. The Hon. Treasurer shall hold office for three years and shall be eligible for re-election. The Treasurer shall keep the Society's funds. His sanction shall be required for the disbursement of the Society's moneys and he shall present a financial statement at the Annual Meeting. The financial status and policy of the Society shall be considered each year at a meeting of the Council held as soon as practicable after the audit. The audited accounts shall be published in the Journals of the Society.

14. The Hon. Secretary shall be responsible for collection of subscriptions.
15. If any Council Member does not attend at least one meeting of the Council during the year he shall retire at the end of the year, but shall be eligible for re-election.
16. At least one fortnight before the Annual Meeting the Secretary shall circulate to all Members of the Society a list of the Members of Council including Officers, indicating those who retire and adding the names of nominees of the Council to fill the vacancies.
17. Members may propose for ballot at the Annual Meeting the name or names of any duly qualified Member or Members in place of any or all of the Council's nominees.
18. The Council shall have power to co-opt any ordinary Member of the Society to fill vacancies occurring during the year among Council or Officers, the tenure of such co-opted Members to terminate at the next Annual Meeting.
19. At the Annual Meeting, after nomination by the Council, persons who have rendered conspicuous service to the subject of Ecology may be elected Honorary Members of the Society.

Such Hon. Members shall receive free either or both Journals of the Society as the Council may determine, and shall also have the other privileges of ordinary members of the Society.
20. The Annual Meeting shall be held in December or in the following January. At least one other Meeting shall be held later in the year. Further Meetings and Excursions may be held at such times and places as the Council may from time to time determine.
21. At the Annual Meeting the Members of the Society present shall elect the Officers and Council, in the case of a contested election by ballot, and consider any other business brought before them by the Council; or business brought before them by any Member, of which four weeks' notice in writing has been given to the Secretary.
22. Alterations of the Rules shall only be made at the Annual Meeting and require six weeks' notice in writing to the Secretary and a majority of two-thirds of the Members voting.
23. Members desiring to present communications at any Meeting must give due notice to the Secretary, stating the nature of the communication and the time required.
24. At any Meeting of the Society the Chairman shall decide as to procedure and the order of business. It shall be within the Chairman's discretion to admit communications or other business, other than alterations to the Rules, not included in the programme.
25. A Meeting of the Council to consider the Annual Report shall be held shortly before the Annual Meeting.
26. The Society shall issue two Journals, *The Journal of Ecology*, and *The Journal of Animal Ecology*.
27. The subscription price of each Journal to others than Members of the Society shall be as determined by the Council.
28. No Member shall be entitled to receive the Journals of the Society whilst his subscription is in arrear.

(This revised formulation of the constitution and rules was accepted at the Annual Meeting of the Society, January 4th, 1936.)

## LIST OF MEMBERS (JANUARY 6th, 1936)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, DR H. GODWIN, Botany School, Cambridge.

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CONTRIBUTIONS TO THE AUTOECOLOGY OF  
*MERCURIALIS PERENNIS* L.<sup>1</sup>  
 PARTS IV AND V<sup>2</sup>

BY THE LATE S. K. MUKERJI, D.Sc. (LOND.)

(With Plate XII and seven Figures in the Text)

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PART IV. EFFECT OF SOIL FACTORS ON DISTRIBUTION AND GROWTH

WITH the object of studying the effect of hydrogen-ion concentration on the distribution and growth of *Mercurialis perennis* in Britain, the pH values of more than 200 samples of soils in which dog's mercury was growing were determined. From each spot at which the soil samples were taken the fresh weight, dry weight, ash content and average height of 100 leafy shoots of the plant were determined, and the data plotted against the pH values or the specific acidities of the soils. A number of experiments were also carried out in the laboratory to investigate the effect of hydrogen-ion concentration on the growth of both roots and shoots of this plant.

<sup>1</sup> Part of thesis approved for the degree of Doctor of Science of London University.

<sup>2</sup> Parts I-III appeared in this *Journal*, 24, 38-81.

## HYDROGEN-ION CONCENTRATION OF THE SOIL

The soil samples were collected chiefly from a depth of 0–20 cm., because the root system of *M. perennis* attains its greatest development in this region of the soil. 5 gm. of each soil sample were allowed to soak overnight in 50 c.c. of specially prepared water neutral to brom-thymol-blue in a porcelain dish. The measurement of *pH* value was done early next morning partly by the electrometric but mostly by the colorimetric method, since a comparison of determinations of twenty-one English soils of widely different nature by the two methods showed that in four cases the result was the same to the first decimal place, in six it differed by 0.1, in nine it differed by 0.2, and in only two did it differ by as much as 0.3.

Most of the soils examined showed a strong buffer action. In the majority of woodland soils in Britain, slight additions of acids or alkalies would not therefore bring about any deviation of the actual hydrogen-ion concentration of the soil. There are, however, exceptions to this. The sandy soils of the Lower Greensand of Westerham in Kent, for instance, show a much slighter buffer action than the clayey soils of Orpington or the humus soils of Purley Beeches (Surrey). This buffer action of the soil, which is due to several factors, including soil colloids and the presence of various bases in excess, must be of considerable importance to any natural vegetation. Marked fluctuations from time to time in the hydrogen-ion concentration of a particular habitat would certainly impair the growth and stability of some species. Though many plants have a considerable range of hydrogen-ion concentration within which they will grow there are limits beyond which growth suffers or becomes impossible.

In order to test the variation in *pH* value of the upper layers of the soil of an apparently homogeneous habitat, such as that of a given type of beechwood or oakwood, fifteen soil samples from the top 15 cm. were collected in a beechwood at Woldingham (Surrey) at intervals of about 10 metres. Of the fifteen, two samples gave a value of 5.7, two of 5.8, five of 5.9, one of 6.0, three of 6.1, and two of 6.2, a total range of only 0.5. Of five samples from an ashwood at the same place three showed a *pH* of 7.2, one of 7.3 and one of 7.4. From a yewwood on Boxhill in Surrey, five samples ranged from 5.4 to 5.6. Nine samples from an oak-hazel coppice at Orpington ranged from 6.2 to 6.6. But if a homogeneous piece of woodland is altered by partial felling or coppicing, thereby allowing more light to penetrate in certain areas than in others, the hydrogen-ion concentration of the soil correspondingly shows marked differences at different spots within the same general habitat. The soil of hollows in which leaf litter has accumulated and of other places with high humus content usually give a more acid reaction than those collected from the rest of the woodland. Thus, in such a hollow in the yewwood on Boxhill, of four samples one showed *pH* 4.5 and three *pH* 4.6, as contrasted with 5.4–5.6 from the general soil of the wood.

The hydrogen-ion concentration of soil samples collected from the same locality at different times of the year showed no well-defined seasonal variations.

A feature of British woodland soils is the stratification of soil reaction caused by leaching and by surface humus formation. Salisbury in 1922 established this fact with abundant data, and the results obtained at different depths (Table I) in the present work corroborate his conclusions.

Table I. *Stratification of pH and organic content*

	pH	Loss on ignition %		pH	Loss on ignition %
Pteridetum (Kingsley):			Pinetum (Boxhill):		
0-15 cm.	4.9	11.5	0-15 cm.	5.4	12.2
15-30	5.6	7.1	15-30	5.9	7.5
30-45	6.1	5.6	30-45	6.6	3.2
Pteridetum (Lower Evans):			Oakwood (Staplehurst):		
15-30 cm.	4.2	5.7	0-15 cm.	6.2	18.8
45-60	6.1	1.9	15-30	6.9	15.6
			30-45	7.4	12.8
Oakwood (Coulsdon):			Purley Beeches:		
0-15 cm.	6.6	10.5	0-15 cm.	6.8	12.6
15-30	7.1	7.3	15-30	7.2	8.5
30-45	7.4	4.1	30-45	7.6	5.7

*pH values in relation to nitrate, organic, and calcium  
carbonate contents of the soils*

It has been shown by several workers (e.g. Olsen, 1921) that nitrification is absent or extremely slight in the most acid raw humus soils, and the plants which habitually grow in such soils mostly utilise ammonia which occurs in considerable quantities. My analyses of a very large number of soil samples show that the nitrate content is as a rule higher in a soil which gives only a slightly acid or a neutral to alkaline reaction. Soils with a pH value below 4.2 are extremely poor in nitrates, while those above pH 5.0 show varying degrees of nitrate content with the diphenylamine test. This is, of course, intelligible in the light of recent researches in which it has been shown that the most active of the nitrifying micro-organisms of the soil cannot thrive in very acid soils, flourishing best in soils which are slightly acid or neutral to alkaline in reaction (cf. Russell, 1927).

Table II. *pH value, nitrate, organic and total carbonate content*

Soil samples	pH	Nitrate content	Organic content	Total carbonate %
0-15 cm.				
Hedgebank (Westerham)	6.9-7.1	+	5.6	1.33
Purley Beeches	7.2	+++	12.3	13.8
Pinetum (Boxhill)	5.2	±	8.5	1.6
Taxetum (Boxhill)	5.5	++	9.6	10.2
Oakwood (Coulsdon)	6.6	++	10.6	1.1

The intensity of the nitrate reaction does not, however, bear any definite relation to the increasing pH value (see Table II). For instance, a certain soil

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having as low a *pH* value as 5.6 may give a very high nitrate reaction (e.g. + + + + value), while another with a higher *pH* (6.9) may be poor in nitrate content (+ value). On the other hand, a soil with *pH* 5.4 may show a slight nitrate content (+ value), while another with *pH* 6.8 may give a very high nitrate reaction (+ + + + value).

The potassium and phosphate contents of the soil also have been shown by several workers to have no marked correlation with the hydrogen-ion concentration. But very acid soils, as is well known, often have a markedly low calcium content as measured by total carbonates, almost all the carbonate present being normally calcium carbonate, though calcium may exist in soils in other forms.

With regard to the organic content of the soil (as represented by loss on ignition) it is found that an increase in *pH* (i.e. a decrease in acidity) is generally associated with a decrease in organic content at increasing depths of the soil through the top 60 cm. (Table I). This fact has also been emphasised by Salisbury (1922).

### *Hydrogen-ion concentration and the distribution of Mercurialis perennis in nature*

A number of workers have shown that the composition of the natural vegetation of a habitat depends a good deal upon the hydrogen-ion concentration of the soil. It has already been mentioned that every species has its particular (though often a wide) range of *pH* within which alone it can grow. The range within which *M. perennis* normally occurs in the woodland soils of Britain, lies between *pH* 4.5 and 8.5. Soils outside these limits are in most cases completely devoid of the plant. Within this wider range again there is a narrower one—between 5.8 and 7.2—in which *M. perennis* attains its greatest abundance.

Table III. *Correlation of pH value and the occurrence of  
Mercurialis perennis in Pteridatum near Boxhill*

	Patch A <i>M. perennis</i> present	Patch B <i>M. perennis</i> absent
Average height (cm.)	15	—
Fresh weight (100 shoots) (gm.)	75	—
Dry weight (100 shoots) (gm.)	6.7	—
Ash content (%)	11.2	—
<i>pH</i> of soil	5.3	4.1
Natural water content	27.0	26.1
Loss on ignition (%)	12.6	12.6
Nitrate content	Marked	Marked
Total carbonates (%)	2.5	2.5
Light intensity (%)	37.0	37.0

That hydrogen-ion concentration of the soil is closely correlated with the distribution of *M. perennis* in wild stations will be clear from Table III. During the course of field experiments near Boxhill in May 1926, it was found that there were two adjoining areas, in one of which *Mercurialis* grew while

in the other it did not. Analyses of soils from these two adjoining areas revealed the fact that such important edaphic factors as natural water content, organic content, nitrate and total carbonate content, as well as light intensity, were practically identical in both, the only marked variation being in the hydrogen-ion concentration (Table III). We can only conclude that the soil of Patch B is too acid to support a growth of *M. perennis*.

There are extensive tracts of beechwood in Epping Forest and also near Westerham and Sevenoaks where the surface soil is very loose and consists largely of raw humus and no ground vegetation of *M. perennis* can be found. Soils were analysed from these localities and the light intensity was measured both during the "light phase" and the "shade phase". Readings of soil temperature were also taken during the growing period in the spring. In these woodlands it was found that only low light intensity and high hydrogen-ion concentration, to some extent correlated with humus content, could be supposed to inhibit the growth of *M. perennis* (see Table IV). Though the light intensity was low (3.6 per cent.) this percentage is known from other localities to allow the existence of the female plant.

In some of the coppiced areas adjoining such beechwoods, where more light reaches the ground and the pH of the soil is markedly higher, small patches of *Mercurialis* are found.

Table IV. *Effect of pH and light intensity on occurrence of Mercurialis*

Soil samples 0-15 cm.	<i>M. perennis</i>	pH of soil	Natural water content	Loss on ignition	Nitrate content	Total carbon- ates	Light intensity (shade phase)
Beechwood (Epping Forest):							
Coppice	Present	6.8	38.5	12.7	+ to ±	0.13	23-25
High forest	Absent	3.9-4.1	41.0	16.2	±	0.15	3-5
Beechwood (near Westerham):							
Coppice	Present	5.8	25.0	10.3	±	0.19	10-12
High forest	Absent	4.2	30.0	18.6	±	0.3	4-6

*Experiment to show the effect of pH value of the soil  
on the growth of Mercurialis perennis*

Six comparable samples (i.e. of approximately equal weight and height) of young plants of *M. perennis*, derived from a common parent, were planted separately in six glass jars, each containing a portion of the same soil, viz. peat two-thirds and sand one-third. These jars were mounted in a row on a wooden stand as shown in Pl. XII, phot. 1, each jar being provided with an outlet at the bottom for drainage. Particular care was taken that the same amount of distilled water was added to each jar. The drainage water was collected in separate porcelain dishes, and this was always poured back into its particular jar after having been made up to a fixed volume (75 c.c.) with distilled water, thereby ensuring the return to each vessel of any mineral salts or organic matter that might have been washed down with the drainage water.



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At the beginning of the experiment the soil of each jar was carefully analysed, and it was found that the total carbonate, nitrate and organic contents and also the total water-holding capacity of the soil samples in every one of the jars was exactly the same. The hydrogen-ion concentration was also measured separately and was found to be pH 4.0-4.1 in every case.

In about 5-6 weeks' time when the plants had established themselves, the pH of the soil in five out of the six jars was raised, by the addition of the requisite quantities of sodium hydroxide, to a series of progressively higher values, and it was ultimately found to remain as shown in Table V.

In March, 1927, the plants in each vessel produced a fresh crop of shoots and roots, and a distinct gradation in the height and number of shoots and in root development became apparent in the successive jars (Table V and Pl. XII, phot. 1).

At the end of the experiment, when the plants had ceased growing, the fresh weight, the dry weight, the ash content and the height of the shoots in the respective jars were determined. Soil samples were once again analysed and it was found that all the principal factors, except the hydrogen-ion concentration, had remained the same.

Table V

Jars	pH of soil	Fresh weight of shoots (in gm.)	Dry weight of shoots (in gm.)	Ash content (% of dry weight)	Average height of shoots (in cm.)	Rooting depth (in cm.)
1	4.0	0.62	0.15	10.5	12.5	10.0
2	4.6	1.94	0.46	10.7	15.5	11.2
3	5.2	2.1	0.48	10.7	16.2	12.3
4	5.6	2.9	0.91	10.8	18.7	14.6
5	6.2	2.4	0.78	11.2	20.1	15.1
6	6.7	3.7	0.96	11.3	21.7	16.4

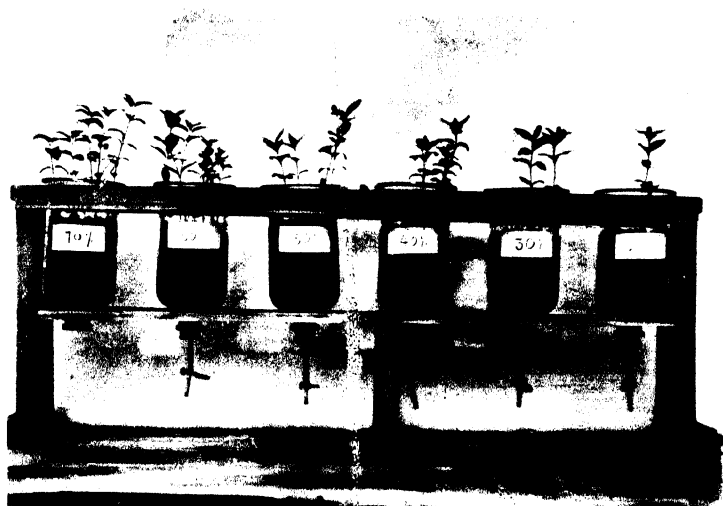
### *Dry weight of the plant and specific acidity of the soil*

The dry weights of 100 shoots of *M. perennis* collected from each of numerous stations<sup>1</sup> were plotted against the specific acidity of the soils from which they were gathered (Fig. 1). It will be seen that all the higher dry weights correspond to locations where the soil reaction approaches neutrality. The lower values, on the other hand, correspond to locations of high specific acidity. It is true that low values, but appreciably higher than the minimal values, are encountered on the alkaline side, but having regard to the relatively large number of locations with a reaction near the neutral point extremes are naturally more likely to occur in this region. From Figs. 1 and 2 the negative correlation between the dry weight and the specific acidity is quite evident.

<sup>1</sup> It is to be noted that in the observations summarised in this and several subsequent figures the author says nothing about the method of choice of sample stations. The graphs cannot therefore be taken as representing random sampling of the conditions to which *M. perennis* is subject in nature, and the loci have individual value only, though it is possible that their distribution may correspond roughly with the total distribution of the plant. EDITOR.



Phot. 1. Effect of hydrogen-ion concentration of the soil on the growth of *Mercurialis perennis*. The pH values of the soils are shown on the labels.



Phot. 2. Effect of high water content on the growth of *M. perennis* in acid peat (pH 4 to 4.1). The percentages of distilled water added are shown on the labels.



## TOTAL CARBONATES OF THE SOIL

As is well known, the action of calcium carbonate on the soil is partly of a chemical, partly of a physical nature. It has a neutralising effect on soil

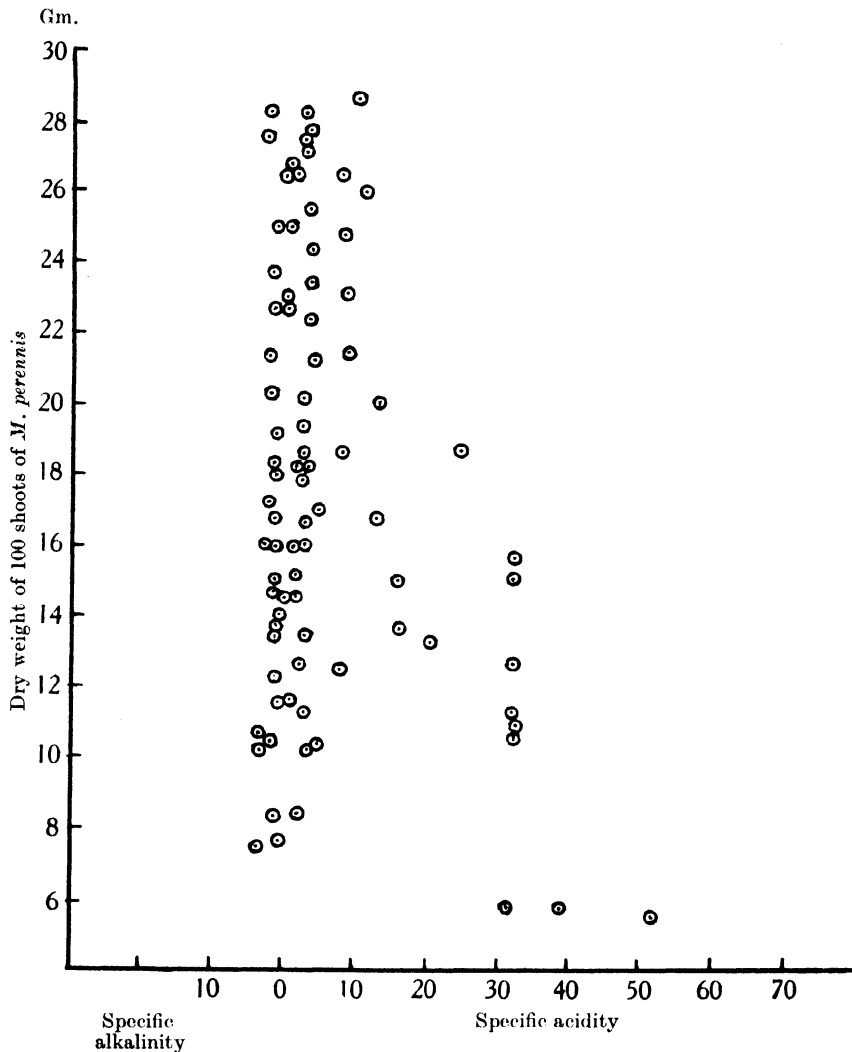


FIG. 1. Dry weight of shoots and specific acidities of soils. Each locus represents 100 shoots.

acids, diminishes the toxicity of certain salts and flocculates the clay fraction, thus improving the texture of the soil.

In order to find out the effect, if any, of the total carbonates of the soil on the occurrence and growth of *M. perennis* in nature, soil samples from about 200 localities were analysed, and at the same time the fresh weight,

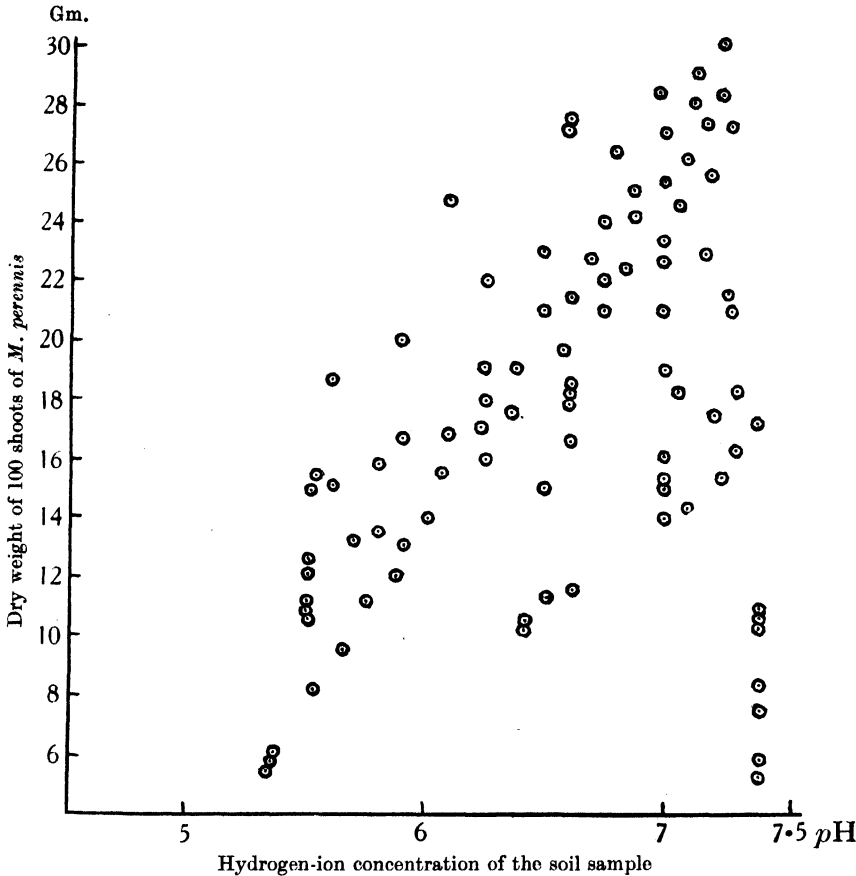


FIG. 2. Dry weight of shoots and pH value. Each locus represents 100 shoots.

Table VI

Locality	Total carbonates (% of dry weight of soil)	Fresh weight of 100 shoots (in gm.)	Dry weight of 100 shoots (in gm.)	Ash content (% of dry weight)	Average height (in cm.)	Fre- quency
Westerham (hedgebank)	0.011	84	11.6	10.1	10	a.
"	0.015	80	10.5	11.1	10	a.
Woldingham	0.07	152	18.2	11.4	15	a.
Staplehurst	0.08	95	13.5	11.2	17	a.
Orpington	0.09	67	10.3	11.2	12	f.
"	0.17	82	18.8	11.7	18	a.
Radlett (hedgebank)	0.97	121.8	18.1	11.7	23	f.
Coulsdon	1.12	150	18.5	12.3	16	a.
Sevenoaks	1.35	60	8.3	10.5	12	o.
Woldingham	11.25	159	24.8	17.6	20	d.
Purley Beeches	13.8	137	17.6	8.9	18	a.
"	25.6	90	10.6	12.8	17	a.
Upper "Warlingham	51.2	80.5	15.2	13.2	15	f.
Boxhill	55.1	170	26.5	18.9	22	a.
"	63.8	25.2	5.8	10.1	10	a.
"	84.2	70	15.1	13.2	12	d.
Woldingham	84.5	85	11.5	10.2	12	a.

dry weight and height of 100 shoots growing in each of these localities were determined. The carbonate content of the soil was measured by means of a Collins calcimeter. After applying the usual corrections the results are expressed as total carbonates per 100 gm. of the soil dried at 100°C. Some of the data are given in Table VI.

The determination of total carbonates (mainly  $\text{CaCO}_3$ ) present in the soil samples collected from wild stations revealed the fact that the total carbonate content is not an important factor in governing the distribution of *M. perennis*. It will be evident from the data given in Table VII that *M. perennis* occurs just as frequently and as abundantly on siliceous soils with extremely low carbonate content (of the order of 0.01 per cent.) as on limestone and chalky soils with extremely high carbonate content varying from 25 to 85 per cent. The plant grows fairly well on sandy soils at Westerham and Oxted which gave a carbonate value of even less than 0.01 per cent. Provided the soil contains a fair amount of organic matter, has a moderate water supply and low acidity, and receives a certain amount of diffuse light, it does not seem to matter, so far as the distribution of *M. perennis* is concerned, whether the soil contains traces of carbonates or has an abundant supply. Thus the presence of carbonates is only of importance indirectly, i.e. because of its effects on the pH value and on texture. Because of its frequent association with chalky and other calcareous habitats, *M. perennis* has often been regarded as a typical calcicole, but this conception requires modification. It is true that dog's mercury is characteristically abundant or dominant on chalky and other highly calcareous soils, but this is not because it needs a high proportion of  $\text{CaCO}_3$  or other carbonates as such, but because it finds there the general physical and chemical conditions best suited for its growth.

*Lime chlorosis.* The presence of excess  $\text{CaCO}_3$  in the soil often produces a kind of chlorotic condition in the leaves of various species including *M. perennis*. The same phenomenon has been recorded by Tansley (1917) in connection with his competition experiments with two species of *Galium*. They turn yellow and do not attain their normal size. Sometimes one side of the leaf grows more vigorously than the other and hence it becomes curved.

The indirect effect of calcium carbonate on the growth of *M. perennis* was demonstrated by the following experiment. A long wooden box with adequate drainage was filled with five different kinds of soil in vertical segments, viz. loam, leaf-mould, peat, chalk and sand. A long piece of mercury rhizome having at intervals shoots of almost equal height was planted in this box in such a way that each kind of soil covered a portion of the rhizome bearing an aerial shoot. This experiment was started on February 25th, 1927, and in about 5 weeks' time the plant had established itself well and had begun to produce both new shoots and new roots in each compartment. An equal amount of distilled water was added to each soil and the box was kept in a greenhouse where conditions of growth were very favourable. By the middle

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of May the shoots that had sprouted in leaf-mould and in peat died, the only ones surviving being in loam, chalk and sand. The shoots grown in loam showed the best growth, then came those in chalk and lastly those in sand.

At the commencement of the experiment, soil from each compartment was analysed and both the hydrogen-ion concentration and the total carbonate content were measured. The data for these two factors are given in the first two columns of Table VII.

Table VII

Soil	pH	Total carbonate content (% of dry weight)	Average height of shoots (in cm.)	Dry weight of shoots (in gm.)	Ash content (% of dry weight)
Loam	6.7	1.25	20	0.6	12.5
Leaf-mould	4.5	0.19	Shoots died		
Peat	4.1	0.25	Shoots died		
Chalk	8.2	85.0	15	0.44	12.2
Sand:					
Initial values (Feb.)	4.8-5.0	1.37	—	—	—
Final values (May)					
Patch A	6.1	1.39	15	0.41	11.1
Patch B	5.0	1.37	10	0.25	10.9

About the third week of May, a marked difference in growth of the shoots in sandy soil became manifest. Here they occurred in two clumps, i.e. Patch A, which had sprouted next to the chalky soil, and Patch B, which grew at the far end of the same compartment, away from chalk. The shoots of Patch A were more vigorous and decidedly taller than those of Patch B (Table VII). On analysis of soil samples from these two patches, it was found that the pH of the soil in Patch A had considerably altered owing to the percolation of alkaline water from the adjacent soil segment (this sandy soil not being so highly buffered as some natural woodland soils), while that in Patch B had remained the same (Table VII). The soil of Patch A now gave pH 6.1, that of Patch B pH 5.0. The carbonate content had also risen though very slightly, Patch A recording 1.39 per cent., while Patch B was the same as before—1.37 per cent. It was therefore evident that other factors of the sandy soil having remained practically the same, a lowering of the hydrogen-ion concentration due to percolation of alkaline water from the adjoining compartment containing chalk, presumably led to the formation of more vigorous taller and healthier shoots. Thus it appears that  $\text{CaCO}_3$  affects the growth of *M. perennis* indirectly by raising the pH of the soil.

The total carbonate content of the soil samples collected under *M. perennis* growing under scrub, along hedgebanks or in various kinds of woodland in Britain showed an extremely wide range, varying from 0.01 per cent. in some sandy soils to about 84 per cent. in some chalky ones. As far as the growth of *M. perennis* was concerned, other factors of the habitat being favourable, the total carbonate content did not seem to exercise any marked influence

on its dry weight, height, or ash content. In fact it was found that, apart from a certain minimum requisite quantity of  $\text{CaCO}_3$  which is essential for healthy development of the plant, the growth of *M. perennis* (as manifested by its fresh weight, dry weight, ash content and height) did not show any definite correlation with either low or high carbonate content. The plants flourished equally well whether they occurred on non-calcareous sandy soils markedly deficient in  $\text{CaCO}_3$  (i.e. containing about 0.01 per cent.), or on highly calcareous chalky soils with a carbonate content of anything up to about 84 per cent. These facts appear clearly from the data given in Table VI (p. 324), where seventeen localities are given in ascending order of the contents of their soils in total carbonates.

#### NITRATE CONTENT OF THE SOIL

The nitrate content of the soil samples collected from about 250 localities in different parts of south-eastern England was determined by the diphenylamine-sulphuric acid method. From each of these localities, numerous bunches of 100 shoots were also gathered on the same days that soil samples were collected. The fresh weight of 100 shoots at a time was taken on the spot by means of a fairly delicate horn balance. The average height, dry weight and ash contents of these were determined later in the laboratory.

Table VIII. *Table showing the growth of Mercurialis perennis in relation to the nitrate content of the soil*

Locality (soil sample 0-15 cm.)	Nitrate content	Fresh weight of 100 shoots (in gm.)	Dry weight of 100 shoots (in gm.)	Ash content (% of dry weight)	Average height (in cm.)
Westerham	±	60	8.3	10.5	10
Staplehurst	±	162	16.1	15.0	23
"	±	251	28.2	18.0	32
Orpington	±	67.2	10.3	10.2	15
"	+	79.8	11.3	11.9	15
Woldingham	++	96.5	13.5	11.2	13
Bricket Wood Scrub	++	121.8	18.0	11.7	23
Purley Beeches	++	80	10.4	10.8	15
"	+++	79	10.3	11.1	14
Boxhill	+++	70	15.1	13.2	14
"	+++	85	15.5	13.4	14
Blackbird Wood	++++	172	26.7	15.4	20
Staplehurst	++++	95	13.2	11.2	16
Coulsdon	++++	135	16.7	11.5	18
"	++++	96.5	13.5	10.8	12

On an examination of the data thus obtained it was found that the nitrate content of the soil evidently exercised little influence on the growth of *M. perennis* in nature. For example, it was observed that 100 shoots of *M. perennis* from localities which gave a very strong nitrate reaction (++++) had approximately the same dry weight and average height as those collected from soils with very low nitrate content (±). Other factors, e.g. organic content, water content, pH of the soil and light intensity, being favourable,



the nitrate content of the soil did not matter. *M. perennis* cannot therefore be said to be a "nitrate-loving plant" in the same sense as *Urtica dioica* (cf. Olsen, 1923). These facts can be clearly seen from the data given in Table VIII, where the soils are arranged in ascending order of their content in nitrates.

#### ORGANIC CONTENT OF THE SOIL

As there is really no accurate method of estimating the organic matter of the soil, for the purposes of this investigation the "loss on ignition" has been used. The analysis of over 200 samples of woodland soils having a ground

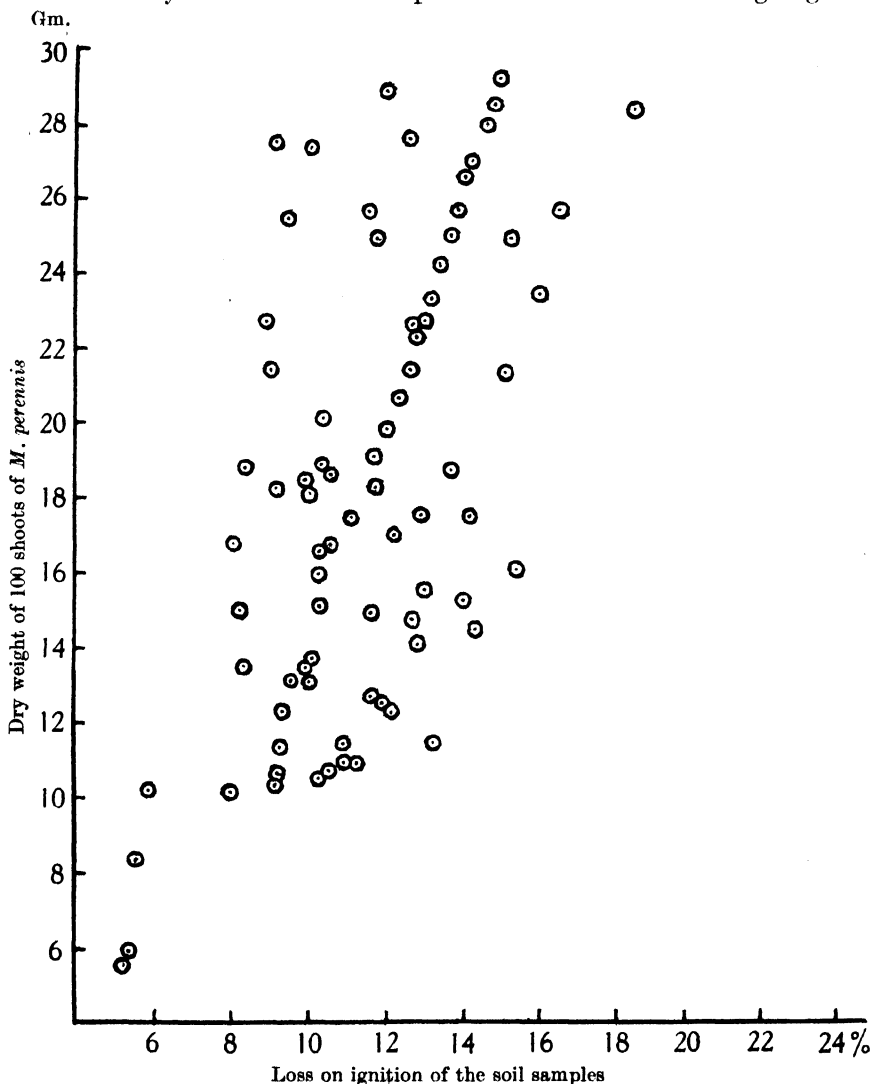


FIG. 3. Dry weight of shoots and loss on ignition of soil samples.  
Each locus represents 100 shoots.

vegetation of *Mercurialis perennis* has revealed the fact that this plant can grow in soils having a range of organic content between 4 and 20 per cent.; but it is usually absent where there is less than 5 per cent. or more than 18 per cent. of organic content (Fig. 3). It will also be evident from Fig. 3 that a definite correlation exists between the loss on ignition of the soil and the dry weight of the shoots of *M. perennis*. A marked increase in the dry weight of the plant takes place with a corresponding increase in the organic content of the soil.

#### WATER CONTENT OF THE SOIL

50 gm. of soil were weighed out, in every case on the spot, in each station. These weighed samples were then wrapped in oiled paper, packed in tins, and brought to the laboratory, where the percentage of water was calculated on the weight of the soil dried at 100°C. An examination of the data collected in different seasons from over 150 localities showed a marked seasonal variation. In spring, the water content is generally from 45 to 60 per cent., after which there is a marked decline, 18–25 per cent. being the average range during the summer when the minimum is reached; the period of duration of the minimal value is of great importance as far as growth of *M. perennis* is concerned. On the whole, calcareous clay shows a higher water content than loam, and this difference is especially noticeable during the summer.

*M. perennis* occurs in soils having a water content of 12–70 per cent.; but its maximum frequency is generally attained in soils containing, during the spring, from about 35 to 55 per cent. of water. As mentioned elsewhere, its distribution in wild stations appears to be closely correlated, *inter alia*, with a number of soil factors besides water content, e.g. pH value. But even when soil reaction is favourable, very low (i.e. less than 10 per cent.) or very high (i.e. more than 70 per cent.) water content of the soil, especially during the spring, may become a limiting factor for the growth of the plant. As a rule, *M. perennis* does not occur in those localities which have a very low water content coupled with high acidity or marked deficiency in light intensity. The plant shows xeromorphic response under conditions of drought, the leaves becoming more hairy and reduced in size and the shoots more stunted than under normal conditions of growth.

Six plants of *M. perennis* were grown in pots containing loamy soil from Orpington, and the wilting coefficient of the soil was determined. It was found that permanent wilting set in when the water content of the soil in six different pots ranged from 12 to 14 per cent. Similar experiments were performed using peaty soil and a higher value was obtained. The wilting coefficient in this case was 18–20 per cent.

It is now generally recognised that the value of the wilting coefficient is dependent both upon external conditions and on soil structure. By ensuring a very gradual drying of the soil, it was found that the wilting coefficient of

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the same loamy soil at Orpington could be lowered from 12 to 9 per cent. Then again, when the hydrogen-ion concentration of this soil was changed from pH 6.8 to 4.4 by the addition of acid potassium phosphate, *M. perennis* showed permanent wilting, even when the water content was maintained at as high a level as 18 per cent. In this case, the high acidity may have been instrumental in hindering the absorption of water by the roots, so that the plant was unable to keep the balance between the amount of water lost by transpiration and that absorbed from the soil, in spite of the fact that the soil

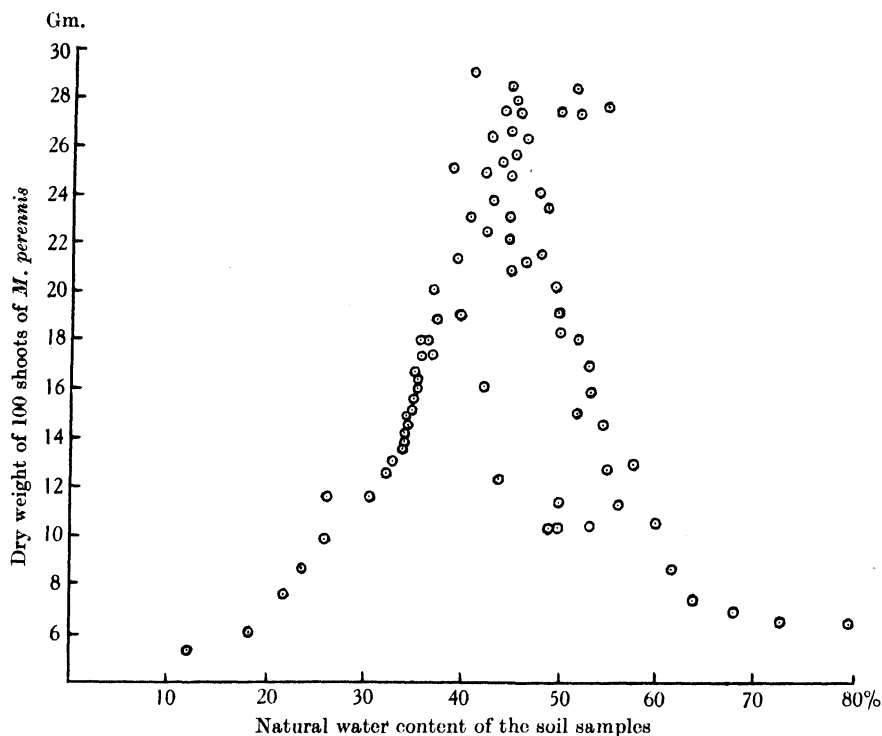


FIG. 4. Dry weight of shoots and natural water content of soil.  
Each locus represents 100 shoots.

still retained sufficient water to be available to it with a soil reaction more normal for the species.

It will be seen from Fig. 4 that the dry weight of the shoots of *M. perennis* increases with increasing water content of the soil up to a certain limit. It reaches its optimum condition in soils having 40–55 per cent. of water, beyond which it shows a rapid decline.

The ash content of the plant also shows a similar increase in soils having from 40 to 55 per cent. of water content, after which it diminishes (cf. Fig. 5).

A well-marked negative correlation has been found to obtain between the ratio of specific acidity to natural water content of the soil and the dry weight

of the plant (Fig. 6). This would seem to suggest that high water content ameliorates the effect of acidity on the growth of *M. perennis*, a suggestion corroborated by the experiment described below.

*Effect of high water content on the growth of M. perennis in acid peat.* Six comparable samples of *M. perennis* of equal weight and height and derived from a common parent, were separately planted on November 25th, 1926, in six glass jars containing acid peaty soil (three-quarters peat and one-quarter sand), each being provided with an outlet for the escape of drainage water.

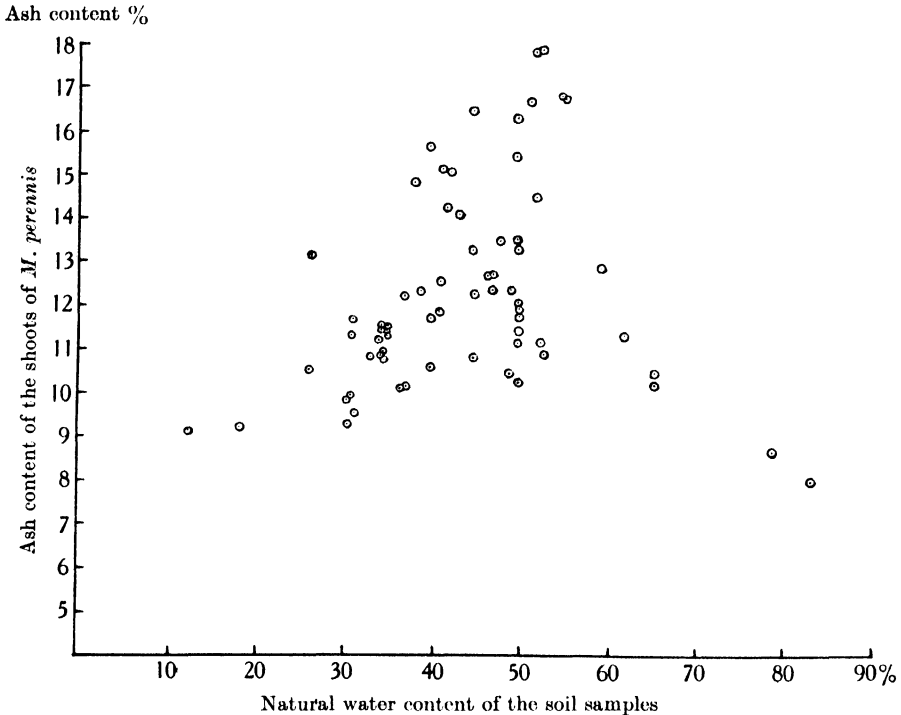


FIG. 5. Ash content of shoots and natural water content of soil.  
Each locus represents 100 shoots.

These jars were mounted in a row on a wooden stand as shown in Pl. XII, phot. 2. At the commencement of the experiment, soil samples from each jar were separately analysed and it was found that the values for the nitrate, total carbonate, organic contents and hydrogen-ion concentration ( $pH$  4.0–4.1) were identical in each case.

When the plants had established themselves in these jars and had begun to produce new shoots and roots a definite amount of distilled water was given to each jar in a regular progressive order from 20 to 70 per cent.

At the end of the experiment in June, 1927, when the plants showed no further growth, the fresh weight, dry weight, ash content and height of the

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shoots produced in the different jars were determined. A striking gradation both in height and in dry weight of shoots was noticeable with the progressive

Table IX. *Effect of different water supplies to Mercurialis growing in acid peat*

pH of all jars 4.1. Nitrate content + Total carbonates 0.21 gm.

Acid peat in jars No. of jars	Water content (%)	Fresh weight of shoots (in gm.)	Dry weight of shoots (in gm.)	Ash content (% of dry weight)	Height of shoots (in cm.)
1	20	0.59	0.14	10.5	12.4
2	30	1.62	0.45	10.7	15.2
3	40	2.21	0.49	10.7	16.4
4	50	3.12	0.95	10.9	18.7
5	60	3.95	1.21	11.5	20.2
6	70	2.87	0.82	10.9	19.5

increase in water content up to 60 per cent., after which there was a fall, especially in weight (Table IX).

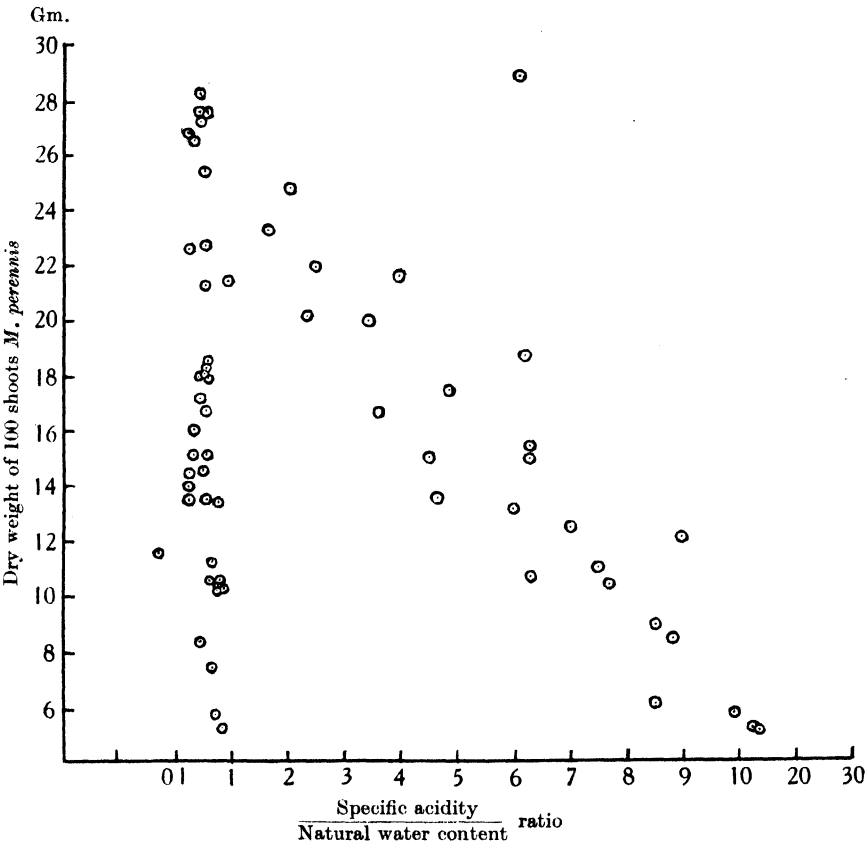


FIG. 6. Dry weight of shoots and ratio of specific acidity to natural water content of soil. Each locus represents 100 shoots.

Up to a certain point, therefore, high water content of the soil clearly ameliorates the bad effect of acidity on this oxyphobe (Fig. 6).

## SUMMARY

The range of reaction of soils naturally bearing *Mercurialis perennis* was from pH 4.5 to 8.2, and optimum development occurred in soils with a reaction round about the neutral point. A negative correlation has been found to obtain between the dry weight and the ratio of specific acidity to water content. Experiments with soils of the same reaction but varying water content confirmed the conclusion that high water content ameliorates the effect of acidity.

The plant shows no correlation between its dry weight and the total carbonate content of the soil, for it occurs with equal vigour and frequency in soils which have a very low carbonate content (i.e. less than 0.01 per cent.) and in soils with a very high carbonate content (i.e. up to about 84 per cent.). The view is therefore expressed that it is not a true calcicole but rather an oxyphobe.

*M. perennis* shows a decided preference for soils having a high organic content, the best growth being obtained in soils with an organic content of 10–18 per cent.

The nitrate content of the soil does not appear to exercise any marked influence on the vegetative growth of the species; but low nitrate content has been shown to bring about retardation, or even in some cases complete suppression, of flowering.

PART V. LIGHT INTENSITY AS A FACTOR IN THE DISTRIBUTION  
AND GROWTH OF THE TWO SEXES

Light intensities were measured by means of an ordinary photographic actinometer, the values being expressed as a percentage of the full sunlight in the open. All the obvious and necessary precautions were taken when working with this instrument.

*M. perennis* is a typical representative of the "shade-flora"; it is unable to flourish in situations with too intense an illumination, or in places fully exposed to the sun, i.e. having no overhead cover or protection of any kind all the year round.

The light intensity often becomes a limiting factor in its distribution even when the other factors of the habitat are entirely favourable. For instance, very high intensities, above 90 per cent., may completely inhibit its growth, for it is almost invariably found that habitats with such intense illumination are entirely devoid of any ground vegetation of *M. perennis*. In the same way, too dense a shade may exercise a markedly detrimental effect on its growth. The lowest intensity of light recorded in a *Mercurialis* society in different kinds of woodlands ranges from 1 to 4 per cent. in the shade phase. This depends upon the type of tree-canopy dominating a particular woodland. Still lower intensities of light cause its entire absence from such situations. The average range of light intensity in a *Mercurialis* society computed from over 250 cases

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appears to lie between 20 and 50 per cent. during the light phase. In the shade phase, of course, these values are very much lower, ranging from about 4 per cent. to about 25 per cent.

#### GREATER TOLERANCE OF SHADE BY THE FEMALE PLANTS

One of the most remarkable features of the species is the degree of specialisation attained by its male and female plants in regard to their respective light requirements. Measurements of light intensity were made in different samples of the *Mercurialis* society occurring in over 250 widely separated localities in Britain. The data have revealed the fact that *the female plants can tolerate far greater shade than the males; these latter, on the other hand, grow most vigorously*

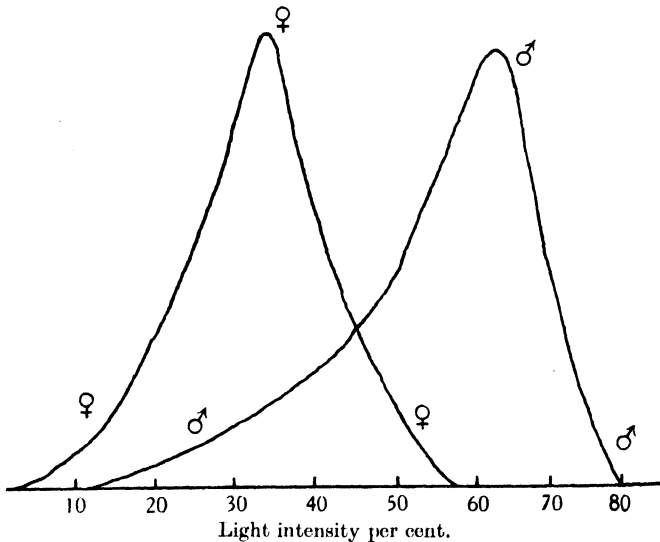


FIG. 7. Ranges of light intensity of male and female plants in the light phase.

*in very much higher light intensities.* The female plants generally occur in the more shaded parts of a beech- or oakwood; sometimes growing exclusively without traces of any male plant in close neighbourhood.

During the light phase the intensity of light in a *Mercurialis* society growing in an oakwood (*Quercetum roboris*) usually ranges between 40 and 60 per cent., but during the shade phase, it seldom exceeds an average of 10 per cent. In a beechwood (*Fagetum silvaticae*), on the other hand, the average intensity during the light phase lies between 25 and 45 per cent., while that of the shade phase is commonly found to be about 4–6 per cent. In the most densely shaded parts of a beechwood during the shade phase it may even drop to about 1 per cent.

Fig. 7 shows diagrammatically and roughly the marked variation in the distribution of the two sexes of this species in relation to their respective light requirements in nature.

Each sex has its own range of light intensity within which it occurs. At the two extreme limits of their respective ranges of illumination, they decrease in numbers till they can no longer subsist under extreme conditions of light, intensity. The male plants are, for example, unable to grow in situations receiving less than about 10 per cent. of light intensity during the light phase, and in the region of higher light intensity they are generally absent from situations receiving more than about 80 per cent. In the same way, the female plants cannot grow in places receiving less than 1 per cent. of light intensity nor in those that receive over 60 per cent. In the middle region of this range, viz. from 10 to 60 per cent., both males and females may occur together, even growing intermixed with each other.

Light intensity, therefore, appears to play a leading role in governing the frequency and abundance of the male and female shoots of *Mercurialis* in wild stations. In situations where the conditions of illumination are favourable for both sexes, i.e. from about 35 per cent. to about 50 per cent., a well-adjusted equilibrium exists between the individuals of the two sexes, and the relative abundance of the members of either sex is masked by this adjustment. But at the two extremes of their ranges of light intensity, members of one or the other sex usually get the upper hand. In lower light intensities the female plants are more successful than the males, while in the higher light intensities the males are more successful than the females. Thus the members of the two sexes very often compete with one another for available space, and it is not unusual for one sex completely to oust the other and succeed in forming its own pure colony. In order to ascertain how far this phenomenon was of general occurrence, over fifty quadrats were marked out in *Mercurialis* societies growing in various types of woodlands, e.g. at Woldingham, Orpington, Purley Beeches and Coulsdon. The small quadrats measured 1 metre square, the larger ones 10 metres square. In every case the respective positions of the male and female shoots were carefully charted. After a close study of these quadrats, it was found that the female plants of *M. perennis* always tended to grow in more or less pure clumps of very varied dimensions. This is brought about by the colonisation and spreading of the underground rhizomes in all directions radially from one or more original female plants, which thus succeed in colonising new ground at the expense of the males, because, as will be shown, lower intensities of light promote a better growth of the females than of the males, both in fresh and dry weight as well as in height. Thus the male plants in dense shade find it extremely difficult to fit themselves into the general structure and economy of the *M. perennis* society as a whole, and hence have to give way to the competition of the female plants in the densely shaded interior of woodlands. This grouping into clumps of the female plants,



however, does not imply that they do not ever occur as isolated individuals outside these clumps. In the intermediate ranges of light intensity, i.e. from 25 to 50 per cent., both male and female shoots grow intermixed with each other, occurring either as isolated individuals or in clumps, the males appearing in patches of females and *vice versa*. The presence of these isolated individuals of one sex in a dense colony of the opposite sex may be accounted for by the fact that they are often produced in nature as a result of the germination of seeds, the seedlings produced being the starting-point of the growth of individuals of the sex opposite to that of the dominants of the colony. Thus, for

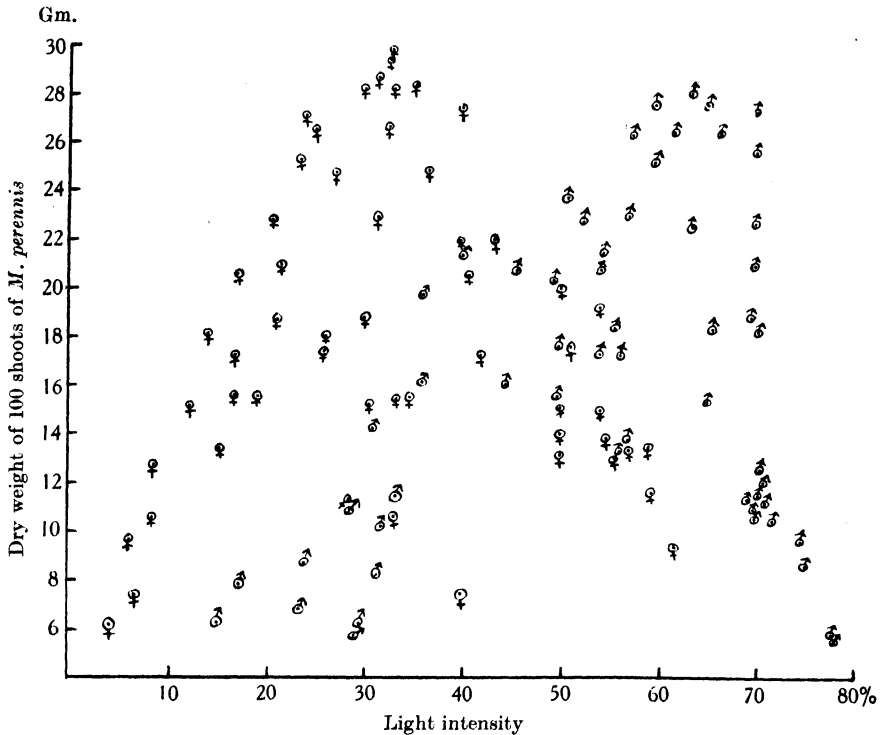


FIG. 8. Dry weight of shoots of male and female plants in different light intensities.

instance, a female plant produced by the germination of a seed, once it takes a hold on the ground and establishes itself in the midst of a colony of male plants, may soon become the nucleus from which new plants may grow in all directions, and these may spread over a smaller or larger area. The great powers possessed by the rhizomes of spreading and colonising fresh areas is remarkable; and in the case supposed the ultimate result would be the production of pure clumps of female shoots in a colony of male plants. In this connection it must be emphasised that natural regeneration by seed is of great importance in this normally dioecious species, for the mingling of individuals of the two sexes is ensured by this process.

Not only is light intensity a paramount factor in the distribution of male and female plants in a given habitat, but their increase in fresh weight, dry weight, ash content and height is closely bound up with the degree of light intensity in which they happen to grow, and the optimum percentage is markedly different for the two sexes.

When the dry weights of equal numbers of shoots (100) of both male and female plants collected from each of about 150 localities was plotted against the percentage of light intensity under which they grew during the light phase (Fig. 8), it was found that the optimum for dry weight in the males was between 50 and 70 per cent. of light intensity, that in the females between 20 and 40 per cent. This suggests that the photosynthetic mechanism or other metabolic processes depending on light in the members of the two sexes must be tuned to function best under different light intensities.

The following observations bring out the same point. An equal number of female shoots (100 in each case) was collected from three distinct spots, all situated in a line running from the margin of Bricket Wood Scrubs (Herts.) to the interior, and the same procedure was repeated in Purley Beeches (Surrey). Soil samples collected from each spot were analysed and it was found that the various soil factors, viz. hydrogen-ion concentration, water content, nitrates, carbonates and organic contents, were almost identical in all, the only marked difference between the habitat factors of the three spots in each wood being the percentage of light intensity which each spot received (Table X).

In Bricket Wood Scrub (Herts.), for instance, locality A received 60 per cent., locality B 27 per cent., while locality C only received 12 per cent. of light. The growth of the female shoots showed a well-marked increase with the decreasing light intensity. The male plants, on the other hand, showed

Table X. *Showing growth of shoots of the two sexes  
in relation to light intensity*

Locality	Light intensity	Plants				Soil (0-15 cm.)					
		Fresh weight of 100 shoots (in gm.)	Dry weight of 100 shoots (in gm.)	Ash content %	Average height (in cm.)	Natural water content %	Loss on ignition %	Nitrate content	Total carbonates %	pH	Soil temp. ° F.
Bricket Wood Scrub (Herts.):											
Female plants											
A	60	91.5	13.6	9.3	15	31	8.03	++	0.97	7.2	43
B	27	108.2	16.8	9.9	19	31	8.16	++	0.97	7.2	43
C	12	121.8	18.0	11.7	22	31	7.14	++	0.97	7.2	43
Purley Beeches:											
A	53	59.5	8.5	8.2	12	45	18.6	++++	13.7	7.4	46
B	40	90	10.6	9.5	15	46	19.2	++++	13.8	7.4	46
C	26	130	17.2	11.9	23	46	18.9	++++	13.6	7.4	46
Staplehurst oak-hazel:											
Male plants											
A	15	20	6.2	8.1	8	52	14.6	++++	0.08	7.1	—
B	35	95	13.2	11.2	15	49	14.9	++++	0.09	7.2	—
C	57	175	21.3	16.7	25	51	14.7	++++	0.09	7.2	—

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the reverse phenomenon, their growth decreased with diminishing light intensity.

In the same way, male shoots were collected from Staplehurst, Purley Beeches, Woldingham, Blackbird Wood (Radlett), and other localities, and their growth showed a progressive increase with increasing illumination up to about 70 per cent. (Table X).

#### INTERGRADATION OF SEX IN *MERCURIALIS PERENNIS*

The phenomenon of the intergradation of sex is, in rare cases, met with in *M. perennis*. It is, however, not so well defined as in the case of *M. annua*, which has been fully worked out by Yampolsky (1919, 1920).

Although *M. perennis* is nearly always dioecious, yet on a few occasions I have observed the appearance of sporadic male or hermaphrodite flowers upon female plants and also of female flowers upon male plants. The occurrence of monoecious plants in this species has been previously recorded by Saunders (1883) and Williams (1926).

#### DETERMINATION OF SEX BY LIGHT INTENSITY

The simplest hypothesis to explain the distribution in nature of male and female plants of *M. perennis* is that the sex is not definitely fixed in the seedling stage, and that intense illumination produces some internal changes in the constitution of the plant body whereby it becomes male. Female plants of *M. perennis* growing on hedge-banks under the shade of *Ilex* or *Crataegus*, in an average illumination of from 20 to 30 per cent., have sometimes been observed to bear male shoots in the more exposed spots where the light intensity exceeded 75 per cent. This production of male shoots on female plants in intensely bright light lends support to the view that light is a decisive factor in the differentiation of sex in this species. It must be remembered that besides the flowers there are other differences between the individuals of the two sexes, such as the structure and size of the leaves, and the degree of green coloration (see Part III, pp. 72-3).

#### SUMMARY

Light intensity is an important factor that governs the distribution and growth of the male and female plants of *Mercurialis perennis* in nature. High intensities of light up to a maximum of about 80 per cent. favour the growth of the male plants, while low intensities up to 40 per cent. favour that of the female plants. The optimum intensities for the male and female plants respectively are about 60 per cent. and about 30 per cent. of full illumination in the light phase. From 40 to 50 per cent. the two sexes are about equally mixed. It seems likely that light intensity is a decisive factor in differentiating sex in this species.

## REFERENCES

- Olsen, C.** "Studies on the hydrogen-ion concentration of the soil and its significance to the vegetation, especially to the natural distribution of plants." *C.R. Lab. Carlsberg*, **15**, 1, 1923.
- Olsen, C.** "The ecology of *Urtica dioica*." *This JOURNAL*, **9**, No. 1, 1921.
- Russell, E. J.** *Soil Conditions and Plant Growth*, 5th ed. London, 1927.
- Salisbury, E. J.** "The oak-hornbeam woods of Hertfordshire. Parts I and II." *This JOURNAL*, **4**, 2, 1916.
- Salisbury, E. J.** "The significance of the calcicolous habit." *This JOURNAL*, **8**, 1920.
- Salisbury, E. J.** "Stratification and hydrogen-ion concentration with special reference to woodlands." *This JOURNAL*, **9**, 1922.
- Saunders, J.** "Monoecious and hermaphrodite *Mercurialis perennis*." *J. Bot.* **21**, 1883.
- Tansley, A. G.** "On competition between *Galium saxatile* L. (*G. hercynicum* Weig.) and *Galium sylvestre* Poll (*G. asperum* Schreb.) on different types of soil." *This JOURNAL*, **5**, 1917.
- Williams, I. A.** "Monoecious form of *Mercurialis perennis*." *J. Bot.* **64**, 1926.
- Yampolsky, C.** "Inheritance of sex in *Mercurialis annua*." *Amer. J. Bot.* **6**, 1919.
- Yampolsky, C.** "The occurrence and inheritance of sex intergradation in plants." *Amer. J. Bot.* **7**, 1920.

# ECOLOGICAL OBSERVATIONS ON THE RAIN FOREST OF MOUNT DULIT, SARAWAK. PART II<sup>1</sup>

By P. W. RICHARDS

(With Plate XIII and one Figure in the Text)

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## III. TYPES OF VEGETATION (*cont.*)

### **Montane rain forest ("Moss forest")**

LIKE most other Bornean mountain tops of moderate elevation, the crest of the Dulit escarpment is covered with a peculiar type of low forest characterised by the enormously thick growth of hepaticae on the undergrowth and the lower part of the tree trunks. This forest no doubt corresponds to the "Temperate Rain-forest" Schimper describes from mountains in West Java, etc. (1903, p. 723, etc.) and to the "Mossy forest", "*Nebelwald*", "*Eugenia-Vaccinium* Formation", etc., of other authors: it seems to represent a climatic climax type widespread in the mountains of the Indo-Malayan region.

In general appearance the Moss forest is totally different from the lowland rain forest, and, as will be shown, the number of species common to the two is extraordinarily small. The top storey of trees, even in the most sheltered places, does not average more than 15 m. high. Seen from one of the peaks of the mountain, the canopy appears much more level than that of the lowland rain forest and of a peculiar vivid, slightly yellowish green (near the colour of a Mediterranean *maquis*). The foliage is small and coriaceous, sometimes box-like or ericoid, rarely laurel-like and never has drip-tips. Bright red or

<sup>1</sup> Part I appeared in this *Journal*, 24, No. 1, pp. 1-37.

purple limply hanging young leaves, which are so characteristic of lowland rain forest, are almost entirely absent.<sup>1</sup> The tree trunks are relatively thick to their height, so that the "etiolated" appearance typical of lowland rain forest is absent. They are often gnarled and bent and never have buttresses, though several species, e.g. *Casuarina sumatrana* Jungh., have stilt roots, and one tree (not identified) had small loop-like knee roots. Cauliflory is quite absent. There are no thick lianes, and tall climbers in general are scarce. Epiphytes of every kind are abundant, mostly growing in or creeping over the luxuriant "moss" which smothers every available surface in the undergrowth. Fallen logs and standing dead trunks are much more frequent than in the lowland rain forest, and these, together with the thick undergrowth, make a dense tangle which is very troublesome to penetrate.

### (1) CLIMATE

No long series of records of climate is available for any Bornean mountain. Our ideas on the Moss forest climate have therefore to be based entirely on the observations of passing travellers, most of which are very fragmentary.

At the High Camp on Mt Dulit (alt. 1230 m.) regular meteorological observations were made from September 9th to 25th and October 1st to 9th. A few isolated observations are also available for days outside these periods, and as the camp was occupied almost continuously from August to November a fairly good general impression of the climate during these months was obtained.

For about 3 weeks (September 7th to about September 25th) during the period of regular observations there was a remarkably fine, dry spell, with much sun and no heavy rain. To judge from the accounts of previous visitors<sup>2</sup> and such evidence as is available, such weather is quite exceptional. While, therefore, the averages of the observations cannot be relied on as typical, the observations during the dry spell are of great interest as showing the climate at one extreme. The instruments were placed in a small palm-thatched shelter with open sides, situated in an open clearing a few metres from the edge of the escarpment.

The *temperature* observations gave the following results:

	° C.	Date
Absolute maximum	28.0	Sept. 22nd
„ minimum	15.0	„ 25th
	Sept. 9th-25th	Oct. 1st-9th
Mean maximum	26.0	26.25
Mean minimum	16.75	17.0
Mean	21.5	21.5
Range of maximum	5.75	3.0
Range of minimum	2.75	3.0
Greatest daily range	12.0	12.0
Mean daily range	9.5	9.25

To nearest 0.25° C.

<sup>1</sup> Only two individual young trees with this type of young foliage were seen in the Moss forest.

<sup>2</sup> **Hose** (1893, p. 204) says: "The wind and mist on Dulit's summit reminded me of a bleak November morning in England."

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The mean temperature is thus  $5.5^{\circ}\text{C}$ . lower than at the Base Camp over almost the same period. Both the mean and the maximum daily range are greater.

There were no means of estimating how much greater the *rainfall* was at the High Camp than at the Base Camp. It was of a rather different character, being usually rather less violent and of longer duration: it was also less limited to a particular time of day. During the dry spell there were about eleven entirely rainless days, three of them consecutive, and on no day was there more than a light shower. Towards the end of this dry spell the surface of cushions of moss at the base of the trees dried up, though the deeper layers remained moist. The ground became much less sodden and swampy than usual, though it never dried up altogether, except at the extreme surface in clearings and other places exposed to the sun.

*Wind* velocities were certainly rather greater than at the Base Camp, but strong wind rarely lasted for more than a few minutes. In spite of the somewhat "wind-swept" appearance of the vegetation, the Dulit ridge cannot be described as "wind-swept", not, at least, by English standards.

The *relative humidity* (hair hygograph) records show that, as at the Base Camp, the air is saturated or nearly so all night. The minimum humidity is reached about midday. During the period October 1st-6th (after the dry spell, but still perhaps drier than normal) the mean minimum humidity was 62 per cent., corresponding to a saturation deficit of the order of 10 mm.<sup>1</sup> During the dry spell (September 9th-25th) the mean minimum was 53 per cent., and on one day it fell to 39 per cent.: the corresponding saturation deficits are approximately 11 and 17 mm. respectively.<sup>1</sup> It is very unfortunate that no figures for the Base Camp over exactly the same periods are available, but the records for October 1st-6th at the High Camp are fairly comparable with those for October 13th-22nd at the Base Camp. The available evidence suggests that though the *average* daily maximum saturation deficit is much smaller at the High Camp, the maximum during dry spells is probably not much less than at the Base Camp. A marked characteristic of the High Camp humidity curves is the large number of sudden oscillations superimposed on the general course of the curve: often they have an amplitude of 10-20 per cent. R.H. Even the night phase is not as dead level as at the Base Camp. These oscillations are presumably mostly due to passing clouds and wisps of mist.

No figures are available for comparing the duration of *sunshine* at the High and Base Camps, but it is clear that during dry spells the High Camp receives very considerable amounts. In September there were at least 4 days with 4 hours or more: on one day (22nd) 9 hours 20 min. was recorded. *Mist* is a feature of the High Camp climate almost entirely lacking in that of the Base Camp. Even on fine sunny days wisps and banks of mist frequently blow

<sup>1</sup> Assuming that the minimum humidity occurs simultaneously with the maximum temperature.

across. It seems, however, to be exceptional for the Dulit ridge to be wrapped in mist all day long without a break. The early morning from before till about 2 hours after sunrise was nearly always clear: this was so even on two days in November during the north-east monsoon. At that time of day the crest of the Dulit ridge and neighbouring high mountains (Laiun, Kalulong, etc.) usually stood like islands above a sea of cloud; later, vertical columns of cloud would begin to rise and gradually blot out the view.

## (2) SOILS

The following soil profiles were examined:

### I. *Near High Camp, Dulit ridge, alt. c. 1230 m.*

Tall closed moss forest, without *Casuarina* or *Tristania*. Surface covered with dead leaf litter about 3 cm. deep.

(19)<sup>1</sup> 0–3 cm. Chocolate brown, sticky mould.

(20) 3–30 cm. Yellowish grey, stiff, sticky clay.

(21) 30–70 cm. Grey clay with a few yellowish mottlings. Texture like (20).

### II. *Near High Camp, Dulit ridge, alt. c. 1230 m.*

Tall closed moss forest: some trees of *Casuarina* and *Tristania* present. Surface covered to a depth of 1–2 cm. with litter of dead twigs of *Dacrydium* and dead leaves, also isolated moss plants (*Mniodendron* sp.).

0–8 cm. Chocolate brown, slightly sticky leaf mould.

(5) 8–20 cm. Brownish grey, soft, slightly sticky clay.

(6) 20–45 cm. Brownish grey, hard, sticky clay, containing abundant sand grains.

### III. *Near Igok Peak, Dulit ridge, alt. c. 1360 m.*

Low, fairly open moss forest: no *Casuarina* or *Tristania*. Surface covered to depth of 2–3 cm. with loose dead leaf litter, *Sphagnum*, etc.

0–32 cm. Brown, friable humus.

(23) 32–62 cm. Brownish grey loam, including lumps of sandstone.

62 cm. Sandstone, apparently bedrock.

### IV. *Near High Camp, Dulit ridge, alt. c. 1230 m.*

Tall open moss forest, with *Casuarina* and *Tristania*. Surface covered with moss (*Acroporium* sp.).

0–53 cm. Slightly sticky, chocolate brown leaf mould.

(3) 53 cm. Permanent water table. Yellowish grey sand below.

### V. *Dulit ridge, alt. c. 1300 m.*

Open moss forest, with *Casuarina* and *Tristania*. Dead leaf litter and moss on surface, 3–4 cm. deep.

0–48 cm. Chocolate brown, slightly sticky mould.

(8) 48–56 cm. Sticky, yellowish grey clay.

Water table at 56 cm.: on a later date at 46 cm.

<sup>1</sup> The numbers in brackets are the reference numbers of the soil samples.



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#### VI. *Summit ridge of Dulit, near Igok Peak, alt. c. 1350 m.*

Low open moss forest, verging on "scrub" facies. Litter of dead leaves and *Sphagnum* about 4 cm. deep.

0-43 cm. Slightly sticky, blackish brown humus.

(25) 43-70 cm. Friable, very slightly sticky, greyish brown loam.

70 cm. Sandstone (bed rock).

The soil samples gave the following results on analysis:

Profile	No. of soil sample	Depth in cm.	Comber colour	pH	Organic matter %	Moisture at "sticky point" %	Percentage of sand (1.0-0.04 mm.)	Index of texture
I	19	0- 3	Pink on standing	4.8	7.97	33.9	58.5	16
	20	3-30	"	4.8	1.16	26.2	60.0	14
	21	30-70	"	4.8	3.87	26.2	73.5	12
II	5	8-20	Colourless	4.5	3.17	24.4	80.8	8
	6	20-45	"	4.4	3.93	24.2	71.5	10
III	23	32-62	"	5.0	5.33	30.6	81.3	14
IV	3	53 downwards	"	4.2	2.31	Nil	87.8	0
V	8	48-56	"	4.6	13.06	27.3	70.0	13
VI	25	43-70	"	4.4	15.42	32.2?	71.3	18

Though there is a fairly wide range of variation, these soils have certain marked common characteristics. Most of them are very shallow: in all but one either the parent rock or a permanent water-table is reached at depths much less than a metre. In all there is a thick superficial humus layer—in strong contrast with the lowland rain forest soils—and even in the deeper layers the percentage of organic matter is considerable. The tendency of soils to be richer in organic matter at high altitudes is of course well known and is attributed to the lower temperature which slows down the rate of decomposition relative to the rate at which humus is formed. The reaction to Comber's test is negative or feeble with all the samples, in spite of high acidity, presumably owing to very severe leaching (which is also suggested by the pale colours). In both these respects the Moss forest soils resemble those of the "Heath" forest rather than those of the Mixed forest. The water of all streams rising in the Moss forest is "black".

The Moss forest soils show a considerable range in texture, and variation in the facies of the vegetation is correlated to some extent with variation in soil texture. As might be expected, the floristic resemblance to "Heath" forest is most marked in the facies of Moss forest on the lightest soils.

#### (3) LOWER ALTITUDINAL LIMIT

The most striking feature of the lower altitudinal limit of the Moss forest on Dulit is its extraordinary sharpness. The transition from Heath forest to Moss forest on the Koyan slope takes place in a zone less than 30 m. wide,

though, as has been mentioned, some Moss forest species descend a considerable distance into the Heath forest. On the Tinjar side the boundary between Mixed forest and Moss forest seemed to be just as sharp, though somewhat obscured by the broken nature of the ground. A similarly abrupt lower limit to the Moss forest has been noticed on other mountains in Sarawak<sup>1</sup> and elsewhere, e.g. in the Philippines (Whitford, 1906, p. 659).

On Dulit this lower limit is at about 1100 m. on the Koyan slope and about 970 m. on the Tinjar slope. On other Sarawak mountains it also lies at heights of the order of 1000 m., but in some parts of the Malayan region it is considerably higher,<sup>2</sup> as the following table shows.

Name of mountain	Latitude	Forest type	Height of lower limit m.	Authority
Dulit, Sarawak (4th Division)	3° 18' N.	Moss forest	970-1100	Richards
Laiun, Sarawak (4th Division)	3° 18' N.	"	1000 (estimated)	"
Kalulong, Sarawak (4th Division)	3° 6' N.	"	1200-1500	A. W. Moore (oral information)
Mulu (west face), Sarawak (4th Division)	4° 8' N.	"	1150	E. A. A. Shackleton (oral information)
Santubong, Sarawak (1st Division)	1° 21' N.	"	Under 750 (estimated)	Richards
Kinabalu, British North Borneo	6° 7' N.	"Mossy forest"	1525-1830	Gibbs (1914)
G. Belumut, Johore	2° 2' N.	"	840	Holttum (1924)
G. Ranai, Great Natuna Island (Boengoeran)	4° 0' N.	Moss forest	800-1000	van Steenis (1932)
Mt Mariveles, Philippines	14° 20' N.	" <i>Eugenia-Vaccinium</i> Formation"	900	Whitford (1906)
G. Gedeh, West Java	6° 48' S.	" <i>Podocarpus</i> sub-zone"*	1650	Seifriz (1923)

\* It is doubtful how closely this corresponds to "Moss forest" as here understood; judging from Seifriz's description both seem to have many features in common, but the trees in the "*Podocarpus* sub-zone" are apparently much taller than usual in Moss forest. Van Steenis (1932, p. 176) says Moss forest in Java begins at 1500 m. and commonly even higher.

The height at which Moss forest begins seems to have no relation to latitude. It does, however, seem to be lower on small, isolated mountains than on large mountain masses.<sup>3</sup> If this proves to be the case, it would seem to be a parallel phenomenon to the "*Massenerhebung*" of the tree-line on the larger *massifs* of the Alps.

<sup>1</sup> The boundary seemed to be much less sharp on Santubong, as far as could be seen on a very hurried visit.

<sup>2</sup> Some individual species common in the Dulit Moss forest are also found only at very much higher altitudes on other mountains, e.g. *Phyllocladus*, which is abundant down to the lower limit of the Moss forest, and even extends down to 750 m. in the Koyan "Heath" forest, does not occur below 1830 m. on Kinabalu (Gibbs, 1914, p. 195).

<sup>3</sup> Mr R. E. Holttum tells me he believes the type of Moss forest met with on large mountain ranges is somewhat different from that met with on more isolated mountains.

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It is usually supposed that this sharply limited Moss forest corresponds with an equally sharply limited "mist zone". Though, as has been shown, the Moss forest on Dulit lives under climatic conditions very different from those of the lowland rain forest, there was little indication of an abrupt change of climate at the boundary or of a definite mist zone. The question, however, is not one which can be adequately studied in a few weeks.

### (4) STRUCTURE AND FACIES

The Moss forest can be regarded as composed of the following synusiae:

- I. Plants not dependent on others for mechanical support.
  - (1) First storey trees.
  - (2) Second storey trees.
  - (3) Tall shrubs.
  - (4) Dwarf shrubs.
- II. Plants dependent on others for mechanical support.
  - (5) Climbers on second (very rarely on first) storey trees.
  - (6) Climbers on the undergrowth and the lower (mossy) part of the tree trunks.
  - (7) High epiphytes.
  - (8) Low epiphytes.

In addition to these we may distinguish three synusiae consisting mainly of bryophytes, each of which includes some lichens (though lichens are usually few both in species and in individuals), viz. a ground, a high epiphyte and a low epiphyte community. The last of these is especially characteristic of the Moss forest.

The above scheme is even more artificial than such schemes usually are and is only given as a help to clear description. It is characteristic of the Moss forest that the constituent synusiae blend into one another so as to defy any satisfactory scheme of classification. For instance, the distinction between epiphytes and ground flora, which in the lowland rain forest is almost absolutely sharp, here becomes very indefinite. It is not unusual to see trees 3 or 4 m. high growing as epiphytes rooted some distance above the ground. There remain, however, some ground herbs which seem never to grow as epiphytes and some epiphytes which seem never to grow on the ground.

A curious feature of the Moss forest is the almost complete absence of vascular saprophytes (a solitary individual, *Burmannia* sp., R. 1744, was found on wet rocks by a waterfall), though the conditions would appear well suited to them. Parasites are also entirely lacking, excepting the green Loranthaceae.

The Dulit Moss forest is by no means uniform in type. Since, however, the variations do not affect either the structure or the floristic composition fundamentally, it is probably best to regard them merely as facies of a single association. These facies, as already mentioned, seem to be correlated to some



Phot. 1. Moss forest, open facies, Mt Dulit, showing characteristic cone of Hepaticae at base of tree.



Phot. 2. Moss forest, scrub facies, Mt Dulit, alt. c. 1300 m. Note prevalence of small leaves.



Phot. 3. Looking upwards in Moss forest, open facies, Mt Dulit, alt. c. 1230 m. Note various microphyllous trees, *Casuarina sumatrana* Jungh. in centre.



Phot. 4. Moss forest, open facies, Mt Dulit.



extent with variations in soil texture, but differences in exposure and possibly other factors are also involved. They pass imperceptibly one into another and form a complete series from the closed to the most open type, but it will be convenient to describe only the two extreme and one intermediate facies.

(a) *Closed facies*

This type of Moss forest is somewhat less unlike lowland rain forest than the others. Trees of the first storey are about 15–18 m. high on the average and form a closed canopy casting a deep shade (though there are large sunflecks even on the ground). *Casuarina sumatrana* Jungh. (R. 1960) and microphyllous trees in general are scarce. Very few of the larger trees were collected, but the number of species of first and second storey trees is probably larger than in the next facies, though certainly very small compared with either Heath forest or Mixed forest.

The undergrowth is much less dense than in the other facies. There are few species of tall shrubs, so that the shrub stratum is very largely composed of saplings of first and second storey trees. In the smaller undergrowth the commonest species are a *Pandanus*, a small spiny palm, and a small tree fern, *Cyathea recommutata* Copel. (R. 1638). Ground herbs are extremely scarce.

The hollows, full of black, semi-liquid humus, which are characteristic of this type of Moss forest and the next, usually remain bare of vegetation, the genus *Sphagnum*, in accordance with its usually shade-avoiding habit, being absent, except occasionally in openings. The most abundant ground mosses are *Mniodendron* spp.

Rotans (climbing palms) are frequent and there are a few other tall climbers. Species of *Nepenthes*, except *N. Veitchii* Hk. f. (S. 542 and 529), are scarce.

Though all the tree trunks are thickly moss-covered, the growth of mosses is nothing like as luxuriant as in the other facies. The moss covering, however, continues up the trunks to a much greater height, and instead of stopping abruptly at a certain level becomes thinner gradually.

Epiphytes are less abundant than in the next facies, especially the smaller low epiphytes. The only common species of these are *Argostemma* sp. (aff. *A. parvifolio* Benn. R. 2101), *Diplycosia chrysothrix* Stapf. ? (R. 1715 and 1991) and *Trichomanes pluma* Hk. (R. 1062, etc.). Just as epiphytes tended to grow at higher levels on the trees in the Mixed forest than in the "Heath" forest, so here in the Moss forest they grow higher in the closed than in the better illuminated open facies.

The closed facies is found on the more clayey soils with a relatively thin humus layer. It is, however, absent in very exposed positions whatever the nature of the soil; thus it seldom extends to the brink of the escarpment.

(b) *Open facies*

This type of Moss forest, in spite of the permanently waterlogged condition of the soil, has a markedly xeromorphic aspect. The first storey trees are not more than 9–12 m. high. A large proportion of both first and second storey trees are microphyllous, and, as they are fairly widely spaced, the undergrowth is only very slightly shaded and there is no definite canopy. The number of species of first and second storey trees is very small, probably not more than ten or twelve: a large proportion of these are conifers.

There is a large number of species of tall shrubs, including many Ericaceae. Ground herbs are fairly common and the surface of the soil is very largely covered with thin carpets of *Sphagnum sericeum* C.M. (R. 2185) and *S. Beccarii* Hampe (R. 2179 and 2184).

Rotans and tall climbers of all kinds, except *Nepenthes Veitchii* Hk. f. (S. 529 and 542) are extremely scarce. Small climbers, on the other hand, are numerous and abundant. Species of *Nepenthes* (*N. Veitchii*, S. 529 and 542, *N. tentaculata* Hk. f., S. 536, etc., and *N. stenophylla* Mast., S. 530, especially common) are very plentiful and form one of the most striking features of the vegetation.

The immensely thick growths of hepatics on the lower parts of the tree trunks, expanding at their bases into conical masses, are highly characteristic of this and the next facies. The lowermost twigs of the trees and the stems of the shrubs are also thickly covered with them. Considerably more species of bryophytes are found in this facies than in the last.

Perhaps the most interesting feature of the bryophytic vegetation is its remarkably clear-cut horizontal zonation. At a certain height, usually about 2–3 m. from the ground, but varying according to the amount of shelter, etc., the thick mantle of mosses on the tree trunks stops abruptly. Above this level (which we may call the “moss line”) a few species of bryophytes are still present, but they are mostly small and of different species from those found below. They either form thin carpets, closely appressed to the bark and covering the surface very incompletely, or grow in small, very dense tufts: they show well-marked xeromorphic characters (in contrast to most of those below the “moss line”). Large ball-shaped masses of hepaticae (especially *Schistochila* sp.) occur occasionally 1–2 m. above the “moss line”.

The existence of this sharp limit seems to depend on a sudden “kink” in the humidity gradient. Wet- and dry-bulb thermometer readings were taken at various heights above the ground on four different days. The results are given in Fig. 1. The curves clearly indicate that between 1 and 3 m. the saturation deficit gradient changes its course sharply. Thus below the “moss line” the air seems to be stagnant and almost always nearly saturated, above it the humidity of the air varies within wider limits and can fall to relatively low values. It must, however, be remembered that owing to its great water-

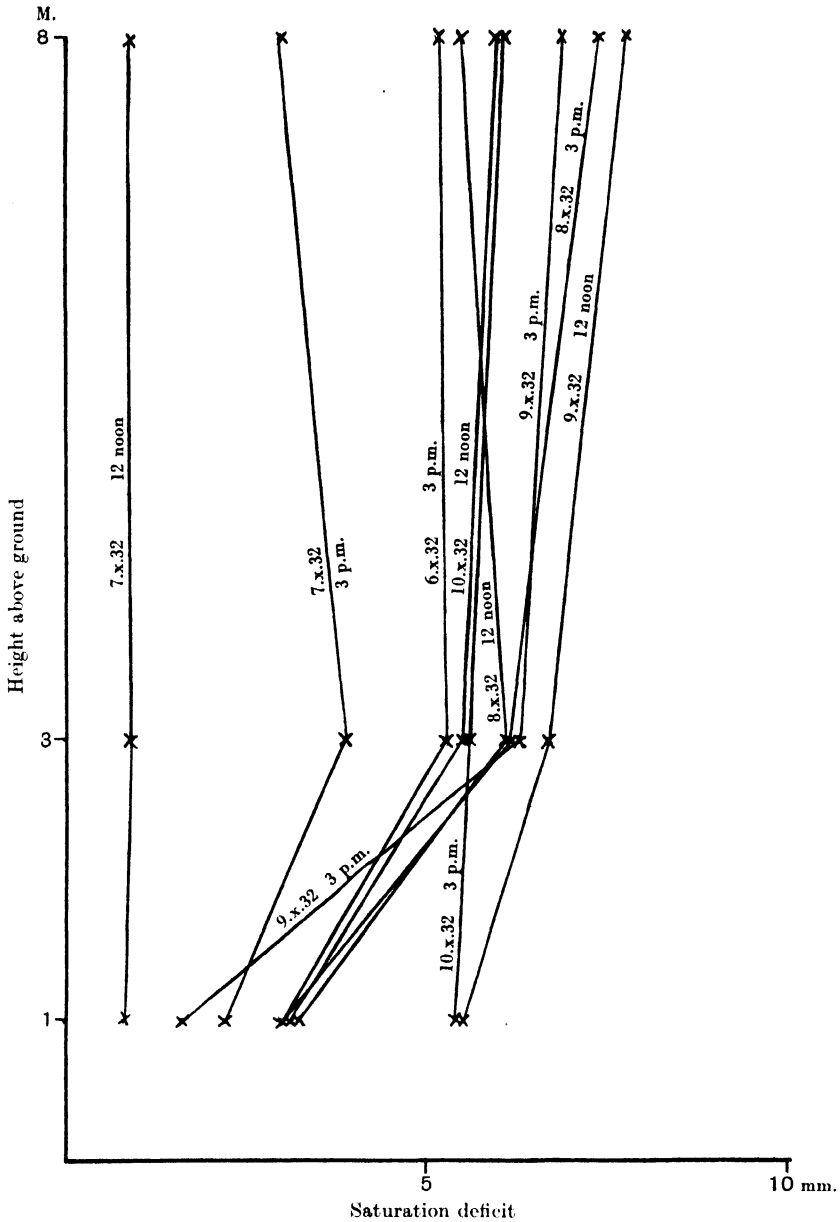


FIG. 1. Vertical gradient of saturation deficit on tree in moss forest, alt. c. 1230 m., Mt. Dulit. Calculated from wet-and-dry bulb whirling psychrometer readings. The weather conditions were as follows: Oct. 6th, weak sun. Oct. 7th, 12 noon, overcast, no sun earlier in the day; 3 p.m., weak sun. Oct. 8th, 12.30 p.m., sun; 3 p.m., sun. Oct. 9th, 12 noon, sun; 3 p.m., sun. Oct. 10th, 12 noon, sun; 3 p.m., sun.



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holding capacity the presence of thick moss in itself tends to keep the atmosphere moist below the "moss line", so that though the "kink" in the humidity gradient may determine the "moss line", the mosses in their turn react on the humidity gradient and make the "kink" more pronounced than it would otherwise be. It will be observed that the type of humidity gradient found here is in contrast with that found in the lowland rain forest, which seemed to fall from 1 m. to the canopy without any well-marked discontinuity.

In the Moss forest the bryophytes are very definitely the dominant epiphytes, so the "moss line" is an important boundary for epiphytes of all other groups. The vascular epiphytes in this facies form two sharply contrasted societies, one of *low epiphytes*, growing in the thick moss below the "moss line", and one of *high epiphytes* on the comparatively bare bark above it. The former consists of shrubs, small climbers, flowering herbs and many ferns, including several species of Hymenophyllaceae of very "hygromorphic" structure. The latter consists of only a few species and almost all of them have markedly xeromorphic characters, e.g. succulent leaves in an orchid, *Bulbophyllum teres* Carr (S. 535), swollen root stocks in *Myrmecodia* sp. (R. 2143) and *Lecanopteris Nieuwenhuisii* Chr. (R. 1811), tomentum on leaves in a common Loranthaceous species, *Notothixos sulphureus* Merrill (R. 1065 and 1238).

Excepting two species which occur rarely as epiphytes on the surface of tufts of hepaticae, lichens are entirely absent below the "moss line": above it they are fairly abundant (*Usnea* sp. (R. 1236), *Parmelia* sp. (R. 1723) and small corticicolous species).

The open facies forms only a small proportion of the total area of the Moss forest on Dulit. It was found on the more sandy soils (which are often very shallow also) and in the more exposed situations.

#### (c) *Scrub facies*

This facies is similar to the last but even more xerophytic in appearance. The tallest trees are under 6 m. high and stand wide apart, so that there is no sort of canopy. The general aspect is that of scrub or *maquis*, rather than forest. The soil is firm and well drained and not waterlogged as in the other facies.

The trees have twisted, bent trunks and comparatively few leaves, an approach to the condition of "elfin wood". Both trees and shrubs have small and usually very coriaceous leaves; many of them have rolled leaf margins, some even have "ericoid" leaves. Trees and shrubs grow together in dense clumps separated by open path-like spaces 1-2 m. wide. In these spaces tussocks of *Cladium undulatum* Thw. (R. 1899) with setaceous rolled leaves grow here and there. The bases of the clumps of trees are buried up to about 1 m. from the ground in tufts of hepaticae of the greatest luxuriance. In these a few of the commonest "low epiphytes" of the last facies are found; above

the "moss line" there are no epiphytes except a few small, highly xeromorphic orchids (*Bulbophyllum teres* Carr, S. 535, etc.).

The flora of this facies is very constant and characteristic. It consists of a small selection of the species found in the open facies with the addition of a few others found nowhere else, e.g. *Cladium undulatum* Thw. (R. 1899), *Gleichenia bullata* Moore (R. 2171), *Hymenophyllum serratum* (Bak.) C. Chr. (R. 2138), and several shrubs. The scrub facies was found on the summits of all the peaks of the ridge, also occasionally on the brink of the escarpment. It nowhere covered any considerable area. The conditions determining it were evidently extreme exposure combined with good drainage and shallow, sandy soil.

#### (5) FLORISTIC COMPOSITION

No sample plots were enumerated in the Moss forest and no estimate of the percentage composition of the tree strata can be given. The following is a list of some of the more abundant or striking species in the various synusia: a. = abundant, r. = rare, Cl. = closed facies, Op. = open facies, Scr. = scrub facies. Where no facies is mentioned the distribution was not specially noted.

##### (a) First storey trees

*Castanopsis* sp., Cl.

*Casuarina sumatrana* Jungh. (R. 1960), Op.

*Dacrydium Beccarii* Parl. (R. 1997 and 1808), Op.

*D. elatum* (Roxb.) Wall. (R. 1962 and 1059).

*D. falciforme* (Parl.) Pilger (R. 1834).

*Horsfieldia* sp. (R. 1667).

*Olea borneensis* Ridl.? (R. 1776), Cl.

*Quercus arbutifolia* Hickel and A. Camus (R. 1885), Cl. and Op.

*Schima*, cf. *S. rigida* Miq. (R. 1698), Cl. and Op.

*Tristania anomala* Merr. (R. 2054).

*Tristania* sp.

*Weinmannia* sp., cf. *Blumei* Planch. (R. 1671).

Various Myrtaceae.

Etc.

##### (b) Second storey trees

*Araliaceae* (R. 1989), Op. and Scr.

*Phyllocladus hypophylla* Hk. f. (R. 1058, etc.), a.

*Podocarpus javanicus* Merr. (R. 1768), seedlings only seen: perhaps a first storey species).

*P. neriifolius* Don (R. 2100), a.

*Vernonia arborea* Ham. var. *magnifolia* Koster (R. 1734).

*V. phanerophlebia* Merr. var. *dulitensis* Koster (R. 1618).

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#### (c) *Tall shrubs*

- Baeckea* sp. (R. 2121), Op. and Scr.  
*Bambusa Gibbsiae* Stapf. ? (R. 2013) (long arched stems, sometimes as much as 10 m. long), Cl. and Op., a.  
*Cyathea recommutata* Copel. (R. 1638), Cl. and Op., a.  
*Drimys piperita* Hk. f. (R. 1645, R. 1896, etc.), Op. and Scr.  
*Euthemis* sp. cf. *E. Engleri* Gilg (R. 2131 etc.), Op and Scr.  
*Ixora acuticauda* Bremek. (R. 1705).  
*I. stenophylla* (Korth.) Kunze (R. 1775).  
*Lasianthus Clementis* Merr. (R. 2098 etc.). Cl.  
*Leptospermum* sp. (R. 1237), Op. (and Scr.?), r.  
*Lycopodium cernuum* L. var. *curvatum* Sw. (R. 1659) (arched stems, 2 m. long), Op.  
*Macaranga* sp.? (R. 2132), Cl.  
*Myrtacea* (R. 1638), Op. and Scr., a.: Cl., r.  
*Neurocalyx pterosepala* Airy-Shaw MS. (R. 1622), Op. and Scr.  
*Oleandra oblanceolata* Copel. (R. 1668), Cl.  
*[Pandanus sp.]*, a.  
*Rhododendron* sp. cf. *crassifolium* Hk. f. (S. 438), Op. and Scr.  
*Rhododendron* sp. cf. *durionifolium*. Becc. (S. 414).  
*Styphelia malayana* (Jack) J.J.Sm. (R. 1619), Op., r.  
*Symplocos Nagelii* (Z. and M.) K. and V. (R. 1669), Cl.  
*Zingiberacea* (R. 1621).

#### (d) *Dwarf shrubs and ground herbs*

- Aeschynanthus* sp.? (R. 2172), Cl. and Op., a.  
*Aracea* (R. 1679), Op.  
*Argostemma* sp. (aff. *A. parvifolia* Benn., R. 2101), Cl. and Op.  
*Cladium undulatum* Thw. (R. 1899), Scr.  
*Dianella* sp. (R. 2051), Cl. and Op., r.  
*Dipteris conjugata* Reinw. (R. 1635), Op.  
*D. Nieuwenhuisii* Chr. (R. 2133), Op., r.  
*Gleichenia linearis* (Burm.) Clarke (R. 2099).  
*G. bullata* Moore (R. 2171), Scr.  
*Isachne javana* Nees (R. 1624), Op., r. (by path only).  
*Matonia Foxworthyi* Copel. (R. 1626), Op.  
*Melastomacea* (R. 2475).  
 Orchids (several species).  
 Palm (R. 1697), a., also several less abundant species.  
*Scleria chinensis* Kunth (R. 1660), Op., r. (by path only).  
*Sonerila* sp. (R. 1842), Cl., r.  
*Taenitis blechnoides* (Willd.) Sw. (R. 1643).  
*Trichomanes pluma* Hk. (R. 1062, etc.), Cl. and Op., r.

## (e) Climbers

*Araliaceae* (R. 1714), Op.

*Artocarpus* sp. (R. 1892), Cl.

*Diplycosia chrysothrix* Stapf? (R. 1895 and 1988), Cl. and Op.

*Embelia pergamacea* A.DC. (R. 2505).

*Nepenthes Reinwardtiana* Miq. (S. 528), Op., r.

*N. stenophylla* Mast. (S. 530), Op. and Scr., a.

Palms (several species), Cl., a.: Op., r.

*Vaccinium* sp. nov. ex aff. *V. camiguinensis* Merr. (R. 1898 and 2124).

## (f) High epiphytes (above the "moss line")

*Bulbophyllum teres* Carr (R. 535), Op.

*Dendrochilum minimiflorum* Carr (S. 548).

*Lecanopteris Nieuwenhuisii* Chr. (R. 1811), Cl. and Op.

*Macrosolen floridus* Danser (R. 1894), Cl.

*Myrmecodia* sp. (R. 2143), Op. (and Cl.?).

*Notothixos sulphureus* Merr. (R. 1065 and 1238), Op., a.

*Polypodium stenopteris* Bab. (R. 2164).

*Rhododendron lineare* Merr. (R. 1982), Cl.

*Trichomanes Schlechteri* Brause (R. 1699), Cl. and Op.

## (g) Low epiphytes (below the "moss line")

## (i) Shrubs.

*Aeschynanthus* sp.? (R. 2172), Cl. and Op., a.

*Rhododendron cuneifolium* Stapf. (R. 1985), Op. and Scr.

## (ii) Small climbers.

*Alyxia pachyphylla* Merr.? (R. 1616).

*Costera cyclophylla* (Airy-Shaw) J. J. Smith et Airy-Shaw, also on ground. etc.

*Diplycosia chrysothrix* Stapf? (R. 1991), a.

*Humata kinabaluensis* Copel.? (R. 2134).

*Lindsaya pectinata* Bl. (R. 1641 etc.).

*Nepenthes tentaculata* Hk. f. (S. 536, etc.), Op. and Scr., a.

## (iii) Herbs.

*Argostemma* sp. (ex aff. *A. parvifolio* Benn., R. 2101), Cl. and Op.

*Coelogyne unguiculata* Carr (R. 2420), a.

*Dendrochilum sublobatum* Carr (R. 2290), Op.

*Elatostemma* sp. (R. 2176), Cl. and Op.

*Hymenophyllum cardunculus* C.Chr. (R. 1704 and 2177).

*H. penangianum* Matt. and Chr. (R. 1707 and 1883), a.

*Scleroglossum crassifolium* (Bak.) C.Chr. (R. 1653), Op., a.

*Sonerila* sp. (R. 2175), Op., a.

*Trichomanes pluma* Hk. (R. 1062, etc.), Cl. and Op., a.

*Zingiberaceae* (R. 1737).

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Two points in connection with the Moss forest flora are worth notice. First, the extraordinarily small number of species common to the Moss forest and the Mixed lowland rain forest. Though the vascular flora of the former amounts to several hundred species and that of the latter to several thousand, less than thirty species were found in both, though a more thorough search would no doubt have revealed more of them. The number of species common to the Moss forest and the "Heath" forest, as has been pointed out, is greater, but is still not very considerable.

Secondly, a strikingly large proportion of the Moss forest flora belongs to the Australasian phytogeographical element. Many of the commonest species, e.g. *Casuarina sumatrana* Jungh., *Drimys piperita* Hk. f., *Phyllocladus hypophylla* Hk. f., as well as many rarer ones, belong to genera of which the "Massenzentrum" clearly lies in Australia and New Zealand. In the "Heath" forest the Australasian element is also represented, though much less strongly; in the Mixed forest it is quite insignificant. The Australasian element is also well represented in the Moss forest flora of most parts of the Indo-Malayan region, but seldom so strongly as on the Sarawak mountains.

#### (6) ECOLOGICAL RELATIONS

The Dulit Moss forest is clearly a type of temperate rain forest. As has been shown, it differs fundamentally from the lowland rain forest in both structure and floristic composition. None of the special morphological features so characteristic of the tropical rain forest, such as buttressing and cauliflory, are found in it. In some respects it might be said to be more similar to a rain forest in New Zealand than to that at the foot of the same mountain.

When we come to consider the relation of the Moss forest climax to the climate determining it, a whole series of problems arises which cannot be solved without experimental study of the physiology of the constituent species and a much fuller knowledge of the Moss forest climate than we have at present.

The most paradoxical of these problems is the fact that though the Moss forest obviously lives normally under conditions of extreme dampness, it has an unmistakably xeromorphic appearance, especially in certain of its facies. There can be no question of an actual shortage of water in the soil at any time, except possibly for short periods in the scrub facies: the soil is normally waterlogged and even in what was probably an exceptionally long dry spell it did not dry up appreciably. The phenomenon is strongly reminiscent of "bog xerophytism" in the North Temperate zone. In each case some sort of hypothetical "physiological dryness" might be assumed, but the well-known experiments of Montfort and Stocker are much against such an explanation as far as temperate bog plants are concerned, and recent workers have regarded their xeromorphy as related rather to desiccating winds in winter. In the

Dulit Moss forest it is unlikely that desiccating winds are a serious factor, since the wind is usually heavily laden with moisture. On the other hand, during dry weather when the saturation deficit of the air rises to comparatively high values the Moss forest (except the lower mossy stratum) would tend to dry up much more easily than the lowland rain forest owing to its openness and the lowness of the trees. Possibly, therefore, the explanation of the xeromorphy is to be looked for in occasional periods of intense transpiration which strain the water-absorbing and conducting powers of the plants.

Whether this is so or not, it should be emphasised that the Dulit Moss forest does not live in an atmosphere which is continuously nearly saturated as Moss forest is generally supposed to do; but, as Holttum has pointed out in his discussion of the Moss forest on Gunong Belumut (1924, p. 256), it occasionally undergoes considerable desiccation, though the soil itself does not dry out.

#### IV. SUMMARY

1. An account is given of the chief types of primary forest in the neighbourhood of a sandstone escarpment (height about 1400 m.) in the interior of north-western Borneo (lat.  $3^{\circ} 19' N.$ ).

2. Two climatic climaxes are recognised, the Mixed Lowland rain forest climax below and the Montane rain forest or "Moss forest" climax above a line running at about 970–1100 m.

3. The Lowland rain forest climate is typically equatorial; the mean temperature being  $26$ – $27^{\circ}C.$  with an insignificant seasonal range, the rainfall heavy and evenly spread through the year, the humidity of the air usually high, though the saturation deficit may be of the order of 12 mm. at midday.

4. The climate of the Moss forest is cooler (mean temp.  $21$ – $22^{\circ}C.$ ) and probably even more humid under normal conditions, though during a dry spell a saturation deficit of as great as 17 mm. was reached. Cloud and mist are characteristic.

5. The structure of the Mixed lowland rain forest is described and illustrated by means of scaled diagrams based on clear-felling plots. Three strata of trees of average heights about 34, 18 and 8 m. respectively are present and below these there is an undergrowth of shrubs, herbs and young trees. Societies of climbers, epiphytes and saprophytes are also distinguished.

Observations were made on the internal climate of the Mixed forest and it was found that the gradients of temperature and saturation deficit were steady without any abrupt change at any level.

The floristic composition of the two taller tree strata was investigated on a sample plot by listing all trees over 8 in. (20 cm.) diam. by their vernacular names. At least ninety-eight species were found on the plot and no one species formed as much as 5 per cent. of the total. A large proportion of the bigger trees belonged to the Dipterocarpaceae.

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6. In addition to the Mixed forest, there was a peculiar type of primary Lowland rain forest on white sand soils which is regarded as an edaphic climax and to which the name "Heath forest" is provisionally given. It differs strikingly from the Mixed forest in the denser, better illuminated undergrowth, scarcity of buttressed trees and very different floristic composition. Sample plots showed that the number of species per unit area was smaller and that there was a marked tendency towards the dominance of a single species, the most abundant species forming 15 per cent. of the total on one plot and 12 per cent. on the other. The conifer *Agathis alba* Lam. was a characteristic tree. This type of forest showed many remarkable analogies to the Wallaba forest of British Guiana.

7. The Moss forest climax clearly belonged to Schimper's class of Temperate Rain forests. The trees were never more than 15–18 m. high on the average and lacked buttresses and other morphological features characteristic of tropical rain forest. The lower parts of the trunks were thickly covered with Hepaticae. In spite of the moist climate the foliage of the trees showed marked xeromorphic features. The floristic composition was entirely different from that of the Lowland rain forest and a large proportion of genera of Australasian affinities was present. A closed forest, an open forest and a scrub facies are distinguished.

### V. APPENDICES

#### A. TECHNIQUE OF SOIL ANALYSES

(i) *Hydrogen-ion concentration.* Quinhydrone electrode method, using suspensions of 1 part soil to 2 parts water, allowed to stand for about 15 hours in a refrigerator. Air dry soil samples collected about ten months previously and sifted through the 2-mm. sieve were used.

(ii) *Organic matter.* The wet combustion method of Sir F. Watt as described by Hardy (1929) was adopted, giving the percentage of organic carbon: this percentage was then multiplied by the arbitrary conversion factor of 1.76 to give the "organic matter". The figures given are the means of duplicate determinations on parts of the same sample.

(iii) *Moisture at "sticky point".* Procedure as described by Keen and Coutts (1928, pp. 745–6), except that samples of 40–50 gm. instead of 10 gm. were used.

(iv) *Percentage of sand.* A conventional beaker method (sedimentation from 7.5 cm. in 75 sec.) used. Soils which contained 5 per cent. or more of organic matter were given previous treatment with 20 vol. hydrogen peroxide. The figures given are the means of duplicate analyses on parts of the same sample.

(v) *Index of texture.* This is calculated as follows:

$$\text{I.T.} = P - \frac{\% S}{5},$$

where  $P$  is the moisture content at the "sticky point" and  $S$  the percentage of sand: it is discussed by Hardy (1928).

*Note.* Altitudes were determined by repeated aneroid readings at Low Camp, High Camp, a series of intermediate points and at the temporary camp in the Kayan valley. Other altitudes were estimated.

## B. ENUMERATION OF SAMPLE PLOTS

Identifications based on material collected on or near plots when collecting number is quoted.

Sample plot 1. Mixed forest, Kapah River (near the Oxford Expedition Base Camp).

Name	Size Class (in.)			Total	As % of all trees 8 in. diam. and over
	8-16	16-24	Over 24		
Arah madu ... ..	2	0	0	2	—
Bawang hutan or Puna (probably <i>Scorodocarpus borneensis</i> Becc., Olacaceae) ...	5	0	0	5	1.9
Berangan batu (probably <i>Lithocarpus</i> , <i>Quercus</i> or <i>Castanopsis</i> sp., Fagaceae) ...	2	0	0	2	—
Biansu bua ... ..	3	0	0	3	—
Biansu pisang ... ..	1	0	0	1	—
Bilian ( <i>Eusideroxylon Zwageri</i> Teysm. and Binn. Lauraceae) ... ..	1	0	0	1	—
Binkuang tapang ... ..	1	0	0	1	—
Binuah ... ..	1	0	0	1	—
Bua ... ..	2	0	0	2	—
Dian or Suloh ... ..	1	1	0	2	—
Dungun puteh ... ..	2	0	1	3	—
Galugut hantu ... ..	1	0	0	1	—
Garang ... ..	2	0	0	2	—
Geronggan or Sarunggan ... ..	1	0	0	1	—
Hilang ... ..	1	0	0	1	—
Impedu ... ..	1	0	0	1	—
Impinit ( <i>Lithocarpus</i> or <i>Quercus</i> sp., Fagaceae) ... ..	0	0	1	1	—
Ipo (probably <i>Antiaris toxicaria</i> Lesch., Moraceae) ... ..	1	0	0	1	—
Jelutong bukit (Apocynaceae) ... ..	2	0	0	2	—
Kabang tiong ... ..	1	0	2	3	—
Kapor paji ( <i>Dryobalanops</i> sp.?, Dipterocarpaceae) ... ..	0	2	1	3	—
Keramoh ( <i>Canarium</i> sp.) ... ..	7	0	0	7	2.7
KerANJI (Leguminosae) ... ..	2	0	0	2	—
Kuminian ... ..	1	0	0	1	—
Kumpang (Myristicaceae) ... ..	1	0	0	1	—
Laban panjang ... ..	1	0	0	1	—
Langer ... ..	2	0	0	2	—
Langsat burung ... ..	2	0	1	3	—
Leban tandok ... ..	1	0	0	1	—
Lun merah or Blaang (Dipterocarpaceae) ...	0	0	6	6	2.3
Luti manggris ... ..	2	0	0	2	—
Malam ... ..	5	0	1	6	2.3
Manggis or Sikup ... ..	1	0	0	1	—
Manggris ( <i>Dialium</i> sp.?, Leguminosae?) ...	0	0	1	1	—
Marakah batu (Dipterocarpaceae) ... ..	1	1	5	7	2.7
Medang baior or M. semarang ... ..	1	1	1	3	—
M. halus daun ... ..	0	0	1	1	—
M. kalah ... ..	7	0	0	7	2.7
M. kapok ... ..	1	0	0	1	—
M. keramoh ... ..	0	1	0	1	—
M. kuning ... ..	1	0	0	1	—
M. langsat ... ..	1	0	0	1	—
M. lit ... ..	12	0	0	12	4.5
M. lunder ... ..	3	1	0	4	—
M. ramin ... ..	0	1	0	1	—
M. ringin ... ..	2	1	0	3	—
M. simpur ... ..	1	1	1	3	—
M. sisit ... ..	6	0	0	6	2.3
M. tangor ... ..	2	0	0	2	—
M. tunjang ... ..	1	0	0	1	—
Medang, Miscellaneous ... ..	2	0	0	2	—



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Name	Size Class (in.)			Total	As % of all trees 8 in. diam. and over
	8-16	16-24	Over 24		
Meranti (Dipterocarpaceae, <i>Shorea</i> sp.?)	2	1	1	4	—
M. daging (Dipterocarpaceae, <i>Shorea</i> sp.?)	3	2	4	9	3.4
M. sabut or Marakah sabut or Boyah (Dipterocarpaceae, <i>Shorea</i> sp.?) ...	1	1	3	5	1.9
Mintangor? (Dipterocarpaceae) ...	3	0	0	3	—
Mora gassin ...	2	0	0	2	—
M. pinang ...	1	1	0	2	—
M. pisang ...	3	0	0	3	—
Mouroh ...	1	0	0	1	—
Niatoh ( <i>Palaquium</i> sp., Sapotaceae) ...	0	0	1	1	—
Nibong ( <i>Oncosperma horridum</i> Scheff.? Palmae) ...	1	0	0	1	—
'Njalín batu... ..	8	1	0	9	3.4
Pangi ...	1	0	0	1	—
Pelajoh ...	3	0	0	3	—
Penaga batu ...	6	0	1	7	2.7
Peter... ..	2	0	0	2	—
P. batu ...	2	0	0	2	—
Puak... ..	4	1	0	5	1.9
P. merah ...	1	0	0	1	—
P. simpoh ...	1	0	0	1	—
Rabah ...	0	0	1	1	—
Rengas (near <i>Melanorrhoea</i> , Anacardiaceae) ...	1	0	0	1	—
Resak peniau (+ R. bukit) (Dipterocarpaceae) ...	2	0	1	3	—
R. sabut ( <i>Kurrimia paniculata</i> Wall.?, Celastraceae) ...	3	1	0	4	—
Samak ...	2	0	0	2	—
Selaut (Annonaceae) ...	2	0	0	2	—
Selekoh (Ammonaceae) ...	2	0	0	2	—
S. puteh (Ammonaceae) ...	3	0	0	3	—
Semourok ...	1	0	0	1	—
Senaga ...	1	0	0	1	—
Soma merah (R. 1604) ...	1	0	0	1	—
S. ramin ...	2	0	0	2	—
Tampar hantu ...	1	0	0	1	—
Tanjan ...	1	0	0	1	—
Tegalam (Dipterocarpaceae) ...	0	0	1	1	—
Tema ...	4	0	0	4	—
T. kulit merah ...	1	0	0	1	—
T. ubah ...	2	0	0	2	—
Toga besih ...	1	0	0	1	—
Ubah ...	1	0	0	1	—
U. kelat ...	6	0	3	9	3.4
U. daun jambu ...	2	0	0	2	—
U. bua ...	2	0	0	2	—
U. milas ...	1	0	0	1	—
U. puteh ...	5	1	2	8	3.1
U. tegalam ...	6	2	1	9	3.4
U. puak ...	2	0	0	2	—
Miscellaneous ...	2	0	0	2	—
Totals ...	199	21	41	261	

## Sample plots 2 and 3, "Heath forest".

S=in swampy part of plot only.

A=absent in swampy part.

	2. KOYAN VALLEY					3. FOREST RESERVE, MARUDI				
	Size class (in.)				%	Size class (in.)				%
	8-16	16-24	Over 24	Total		8-16	16-24	Over 24	Total	
Arang jabu ... ..	1	1	0	2	—	—	—	—	—	—
Bekakal ... ..	—	—	—	—	—	1	0	0	1	—
Berangan batu ( <i>Castanopsis</i> , <i>Lithocarpus</i> or <i>Quercus</i> sp., Fagaceae) ... ..	12	0	1	13	4.0	—	—	—	—	—
B. bras ( <i>Castanopsis</i> sp., Fagaceae) ... ..	—	—	—	—	—	5	0	0	5	1.4
Biansu bukit ... ..	5	0	0	5	1.5	—	—	—	—	—
Bijan ... ..	7	1	0	8	2.4	—	—	—	—	—
B. laki ... ..	—	—	—	—	—	8	0	0	8	2.3
B. suloh ... ..	—	—	—	—	—	4	1	0	5	1.4
Bua ... ..	1	0	0	1	—	—	—	—	—	—
Dahat ... ..	1	0	0	1	—	—	—	—	—	—
Dammar minyak ( <i>Agathis borneensis</i> Warb., R 1919, see pp. 30-1) ... ..	18	7	25	50	15.2	28	8	1	37	10.6A
Dungun api ... ..	0	3	1	4	—	—	—	—	—	—
D. jangkar (Araliaceae) ... ..	1	0	0	1	—	—	—	—	—	—
D. puteh (Araliaceae?) ... ..	0	1	0	1	—	—	—	—	—	—
Gaharu 'nkaras or Buan laki? ... ..	1	0	0	1	—	—	—	—	—	—
Galugu ... ..	5	0	0	5	1.5	—	—	—	—	—
Galugut hantu ( <i>Quercus</i> or <i>Lithocarpus</i> sp., Fagaceae?) ... ..	2	0	0	2	—	2	0	0	2	—
Geredam ... ..	2	0	0	2	—	2	1	0	3	—
Geronggan or Sarunggan ... ..	—	—	—	—	—	2	0	0	2	—
G. petis ... ..	1	0	0	1	—	—	—	—	—	—
Impedu ... ..	3	0	0	3	—	—	—	—	—	—
Impinit ( <i>Lithocarpus</i> or <i>Quercus</i> sp., Fagaceae) ... ..	4	0	0	4	—	2	0	0	2	—
Jagang ... ..	—	—	—	—	—	1	1	0	2	—
Jas (Myrtaceae?) ... ..	2	0	0	2	—	1	0	0	1	—
Kandis ... ..	1	0	0	1	—	2	0	0	2	—
Kapur paia ( <i>Dryobalanops</i> sp.? Dipterocarpaceae) ... ..	—	—	—	—	—	1	0	0	1	—
Katio ... ..	3	0	0	3	—	2	0	0	2	—
Kelumpang ... ..	2	0	0	2	—	—	—	—	—	—
Keruin katap (Dipterocarpaceae) ... ..	—	—	—	—	—	3	0	0	3	—
Koruntum ... ..	—	—	—	—	—	2	0	0	2	—
Kundong ... ..	—	—	—	—	—	1	0	0	1	—
Lalat ( <i>Lithocarpus</i> or <i>Quercus</i> sp.? Fagaceae?) ... ..	2	0	0	2	—	—	—	—	—	—
Langer ... ..	4	0	0	4	—	—	—	—	—	—
Lansi bukit ... ..	1	0	0	1	—	—	—	—	—	—
Luis bukit ( <i>Hopsea</i> sp.? Dipterocarpaceae) ... ..	1	0	0	1	—	—	—	—	—	—
L. galam ( <i>Hopsea</i> sp.? Dipterocarpaceae) ... ..	—	—	—	—	—	7	0	0	7	2.0
Mang or Chengal (Dipterocarpaceae) ... ..	2	0	0	2	—	39	1	0	40	11.4
Manggis or Sikup ... ..	1	0	0	1	—	3	0	0	3	—
Manggris ( <i>Dialium</i> sp.? Leguminosae?) ... ..	—	—	—	—	—	2	2	0	4	—
Marakah batu (Dipterocarpaceae) ... ..	1	1	1	3	—	1	0	0	1	—
Medang ... ..	—	—	—	—	—	2	0	0	2	—
M. bringin ... ..	—	—	—	—	—	1	0	0	1	—
M. kalah ... ..	1	0	0	1	—	—	—	—	—	—
M. kasap ... ..	—	—	—	—	—	1	0	0	1	—
M. katak ... ..	2	0	0	2	—	—	—	—	—	—
M. kuning ... ..	—	—	—	—	—	4	0	0	4	—
M. ladah ... ..	—	—	—	—	—	1	0	0	1	S
M. lawang ( <i>Ternstroemia aneura</i> Miq. R 2658, Theaceae) ... ..	—	—	—	—	—	17	0	0	17	4.9
M. lit ... ..	—	—	—	—	—	2	0	0	2	—
M. lunder ... ..	6	0	0	6	1.8	—	—	—	—	—
M. pasi ... ..	1	0	0	1	—	—	—	—	—	—
M. petis ... ..	1	0	0	1	—	—	—	—	—	—
M. ranin ... ..	4	1	0	5	1.5	—	—	—	—	—
M. ringin ... ..	9	0	0	9	2.4	1	0	0	1	—
M. simpur ... ..	9	1	0	10	3.0	—	—	—	—	—
M. tabak or M. merebong ... ..	—	—	—	—	—	5	0	0	5	1.4S
Mintangor batu ( <i>Calophyllum</i> sp.?, probably Guttiferae) ... ..	12	1	0	13	4.0	17	0	0	17	4.9
M. dudok ( <i>Calophyllum</i> sp.?, probably Guttiferae) ... ..	5	0	1	6	1.8	—	—	—	—	—

# 360 *Ecological Observations on the Rain Forest of Mount Dulit*

	2. KOYAN VALLEY					3. FOREST RESERVE, MARUDI				
	Size class (in.)				%	Size class (in.)				%
	8-16	16-24	Over 24	Total		8-16	16-24	Over 24	Total	
M. jangkar ( <i>Calophyllum</i> sp.?, probably Guttiferae) ...	18	2	0	20	6.1	—	—	—	—	—
Mora pinang ...	3	0	0	3	—	4	0	0	4	S
M. pisang ...	—	—	—	—	—	3	0	0	3	—
M. tuikut ...	—	—	—	—	—	2	0	0	2	—
Mourouh ...	1	0	0	1	—	—	—	—	—	—
Orat matah (Dipterocarpaceae) ...	—	—	—	—	—	4	1	2	7	2.0S
Pangi? ...	1	0	0	1	—	—	—	—	—	—
Peter ...	—	—	—	—	—	0	1	0	1	—
Ramin (near <i>Melanorrhoea</i> , Anacardiaceae) ...	—	—	—	—	—	0	2	1	3	—
Rengas (probably same as one of next three) near <i>Melanorrhoea</i> , Anacardiaceae ...	13	23	5	41	12.4	—	—	—	—	—
R. kusi (near <i>Melanorrhoea</i> , Anacardiaceae) ...	—	—	—	—	—	4	0	0	4	—
R. paya (near <i>Melanorrhoea</i> , Anacardiaceae) ...	—	—	—	—	—	3	0	0	3	—
R. pelandok? (near <i>Melanorrhoea</i> , Anacardiaceae) ...	—	—	—	—	—	7	1	0	8	2.3
Resak bukit (probably includes some of following, probably Dipterocarpaceae) ...	13	0	0	13	4.0	—	—	—	—	—
R. buntun ...	—	—	—	—	—	1	0	0	1	—
R. durian (probably Dipterocarpaceae) ...	—	—	—	—	—	4	0	0	4	—
R. peniau (probably Dipterocarpaceae) ...	—	—	—	—	—	8	0	0	8	2.3
R. rapak (probably Dipterocarpaceae) ...	—	—	—	—	—	1	0	0	1	—
R. sabut ...	—	—	—	—	—	24	2	0	26	7.4
R. tiong ( <i>Vatica</i> sp.?, Dipterocarpaceae) ...	—	—	—	—	—	15	0	0	15	4.3
Ru rapak ( <i>Casuarina sumatrana</i> Jungh., Casuarinaceae) (R. 1873) ...	11	3	5	19	5.7	—	—	—	—	—
Samak masi ...	1	0	0	1	—	—	—	—	—	—
S. ubah ...	0	1	0	1	—	—	—	—	—	—
Selanking ...	—	—	—	—	—	6	0	0	6	1.7
Seluma ...	12	2	1	15	4.6	3	0	0	3	—
Semouruk ...	8	0	0	8	2.4	5	0	0	5	1.4
Serebah laki ...	1	0	0	1	—	—	—	—	—	—
Solunsor ( <i>Tristania</i> sp., Myrtaceae) ...	2	1	1	4	—	8	0	0	8	2.3
Soma ...	—	—	—	—	—	1	0	0	1	—
Tampar hantu ...	—	—	—	—	—	1	0	0	1	—
Tanjan ...	2	0	0	2	—	—	—	—	—	—
Tekam (Dipterocarpaceae) ...	—	—	—	—	—	28	8	6	42	12.0
Tema ...	7	1	0	8	2.4	—	—	—	—	—
Ubah (at least 2 spp.) ...	11	0	0	11	3.3	9	0	0	9	2.6
Totals ...	238	50	41	329		311	29	10	350	
	91					39				

## REFERENCES

- Gibbs, L. S. "A contribution to the flora and plant formations of Kinabalu and the highlands of British North Borneo." *J. Linn. Soc. (Bot.)*, **42**, 1-240, 1914.
- Hardy, F. "An index of soil texture." *J. Agric. Sci.* **18**, 252-6, 1928.
- Hardy, F. "Note on the determination of soil organic matter. A wet combustion method." *J. Agric. Sci.* **19**, 727-33, 1929.
- Holtum, R. E. "The vegetation of Gunong Belumut in Johore." *Gdns Bull. Straits Settlements*, **3**, 245-57, 1924.
- Hose, C. "A journey up the Baram River to Mount Dulit and the highlands of Borneo." *Geogr. J.* **1**, 193-208, 1893.
- Keen, B. A. and Coutts, J. R. H. "'Single value' soil properties: a study of the significance of certain soil constants." *J. Agric. Sci.* **18**, 740-65, 1928.
- Schimper, A. F. W. *Plant Geography upon a Physiological Basis*. Edited by P. Groom and I. B. Balfour. Oxford, 1903.
- Seifrizz, W. "The altitudinal distribution of plants on Mt Gedeh, Java." *Bull. Torrey Bot. Club*, **50**, 283-305, 1923.
- Seifrizz, W. "The altitudinal distribution of lichens and mosses on Mt Gedeh, Java." *This Journ.* **12**, 307-13, 1924.
- van Steenis, C. G. G. J. "Report of a botanical trip to the Anambas and Notoena Islands." *Bull. Jard. Bot. Buitenzorg*, Ser. 3, **12**, 151-211, 1932.
- Whitford, H. N. "The vegetation of the Lamao Forest Reserve." *Phillip. J. Sci.* **1**, 373-431, and 637-82, 1906.

# RELICT SPECIES OF BAS-LANUEDOC<sup>1</sup>

By OLIVE DICKINSON MAGUINNESS

(University of Sheffield)

(With one Map)

IN studying the flora of the south of France in the neighbourhood of Montpellier, I was greatly impressed by the rarity and disjointed distribution of a number of species. It is well known that rarity may be due to a variety of causes. A species may be rare because of its recent origin or recent introduction into a given locality, or the rarity may result from the breaking up of previously continuous areas. The disappearance in intervening places may be due to man's influence, or to natural causes such as geological disturbances, changes in climate, or the natural succession of vegetation. The species with more specialised ecological demands, or with poor means of dispersal, are the most likely to remain rare when introduced or to disappear earlier with changed conditions. Lack of suitable habitat would seem an obvious cause of rarity, and is probably to be considered as a subsidiary cause in very many instances. It has certainly not appeared to be the only or even the chief explanation of rarity in the case of the species I have taken into consideration. The disjointed distribution of many species in Bas-Languedoc suggests survival from a former more continuous one. It will be seen that enquiry into fossil deposits, in order to learn something of past floras of the neighbourhood, was a necessary preliminary to an enquiry into the validity of such a hypothesis.

The floras of the primary and secondary epochs have so little relationship with that of the present day that they cannot throw light on our problem, and we may leave them out of consideration. In the Lower Eocene, side by side with archaic extinct types, we find species which exist to-day in the tropics. Tertiary floras, particularly of the Pliocene, have been carefully studied in the south of France. The work of de Saporta, Laurent, Marty and others has been reviewed and commented on by Depape in 1923 and in 1928. In the Eocene it is evident that there was a lowering of temperature. Here we find several genera of which representatives exist now in the vicinity, and some very few species almost identical with existing ones. The number of genera which are to-day represented in the neighbourhood increases during the Oligocene. Side by side with species of *Pinus*, *Populus*, *Castanea*, *Ulmus*, *Laurus*, *Acer*, *Salix*, etc., we find members of the now exotic genera *Glypto-*

<sup>1</sup> Only very few bibliographical references are given in the text. I have given a complete bibliography of works consulted—Floras, monographs, records of excursions, etc., in *Les espèces survivantes tertiaires du Bas-Languedoc* (Communication No. 31 of the Station Internationale de Géobotanique Méditerranéenne et Alpine, Montpellier, 1934).

*strobilus*, *Zelkova*, *Sequoia*. Depape (1928) summarises the general characters of the vegetation of the Eocene and Oligocene in relation to climate thus: "C'est une végétation où dominant les formes sèches et coriaces développées sous l'influence d'un climat chaud, avec des alternatives très prononcées de saisons sèches et brûlantes et de saisons pluvieuses et tempérées, ressemblant au total à celle de l'Afrique intérieure, avec des traits empruntés à l'Asie méridionale et à la Chine." In the Miocene we still find a mixture of types. The number of northern species increases at the expense of the heat-loving ones, but some tropical plants remain. There is a close similarity between the Pliocene flora and that of the present day. In many instances the species are considered identical. To cite an example from Depape, out of a total of seventy-two species in deposits of the Plaisancian and Astian in the valley of the Rhone, thirty-one are considered identical, and sixteen others almost identical, with existing species. More than half of the species in these deposits are no longer found in the neighbourhood, but most of those which have disappeared exist in other parts of the Mediterranean basin, in slightly warmer latitudes. Marty (1927) suggests that there has been a lowering of mean annual temperature of approximately 4° since the Lower Pliocene. Depape (1928), interpreting his own and others' data, suggests that during the warmest period of the Pliocene (Plaisancian) the mean annual temperature was about 5° higher than now. He suggests also that there was a very much heavier rainfall. The end of the Pliocene and the beginning of the Quaternary mark a crisis for the vegetation. Climatic conditions in Languedoc must at this period have been affected by uplift in the Alpine region. Various deposits indicate that it was a period of violent erosion. It was at this time that the Mediterranean coast of France achieved approximately its present contour. During the Quaternary there were invasions of glaciers, which came as far south in the valley of the Rhone as Lyons, and these were accompanied by great lowering of temperature. There seems to be little doubt that the first of these glaciations dealt the final blow to many heat-loving species in Languedoc. In America and Asia such species could migrate further south, perhaps to re-establish themselves later with return to favourable conditions, but in Europe the retreat was cut off by the barrier of the Mediterranean Sea. I believe that a large number of heat-loving species did, however, escape destruction owing to favourable circumstances, and the species with which my work deals are unquestionably of this character. The Quaternary floras differ from previous ones in the rarity of exotic forms. Subsequently to the rigours of the first glaciation only very few species seem to have disappeared entirely from the flora during the Quaternary period. In many cases, however, the successive advance and retreat of glaciers have influenced migration to south and north respectively. A useful table, showing the probable succession of types of climate and vegetation, has been drawn up by Braun-Blanquet (1923, pp. 28 and 29). Deposits in the form of tufa in the valley of the Lez

near Montpellier, which are assigned by several authors to the last interglacial period, contain more than thirty species. All these species are living to-day, more than two-thirds of them in this same locality, while several of those no longer in the vicinity are found in slightly warmer latitudes. On the whole, however, the changes in flora suggest a climate little different from that of to-day in mean annual temperature, but less extreme and more humid. We know of some species which have disappeared from the flora or changed their area of distribution within historical time, some quite recently. Planchon (1864), Kieffer (1881), and other works furnish useful information.

In brief, we know that during the Tertiary period many species, chiefly thermophile ones, have disappeared from the flora of Europe, and in particular from the area under consideration, and other species have changed their area of distribution. During the Quaternary period, and in recent times, few species seem to have disappeared entirely, but the changes in areas of distribution continue. These changes have led to rarity and disjointed distribution. Palaeontological evidence tells us, then, that the disjointed distribution of at least some species in Bas-Languedoc is due to causes of a historical nature, chiefly changes in climate.

Ch. Martins was apparently the first to comment on this question in relation to Bas-Languedoc. In his work (1871) he remarks that among the plants which suffered heavily from the extreme cold of that winter were some which, though usually considered indigenous because they had been there from time immemorial and propagated spontaneously, were from the point of view of historical plant geography to be considered exotic. This opinion is based on the facts that all their near relatives are exotic, and that their rarity and sensibility to cold suggest that they belong to the flora of a previous epoch of warmer climate. It is further worthy of comment that several of the species which I have reason to believe are relict species suffered greatly during the heavy frosts of the winter 1928-9.

As the area for detailed study I took provisionally the Department of Hérault, which extends from the river Aude in the west to the Vidourle in the east, but I was not strictly limited by the administrative boundaries of the Department. Having found many of the species in which I was interested in the neighbourhood of Narbonne, Leucate, and La Nouvelle, I extended the area to the south and west, making a total area of approximately 3000 square miles (see map). It is a territory particularly suitable for a study of the kind undertaken. It has suffered changes of climate due in part, in the Quaternary period, to the proximity of glaciers, but has never been covered by ice. It is particularly well known floristically, as Montpellier has for centuries been an important centre for botanists. It is therefore extremely unlikely that the species with which I am concerned exist undiscovered in many places, although

my own experience shows that isolated discoveries of species continue to be made in hitherto unrecorded places.

Realising the large number of species which may be considered rare in the flora of this district of Bas-Languedoc, I decided to limit the enquiry to eu-Mediterranean<sup>1</sup> species, although a number of sub-Mediterranean ones may have had a similar history. The *Flore de Montpellier* by Loret and Barrandon (1886) indicates several hundred species as rare or very rare in the Department of Hérault, in the sense of being found in few localities. They may be abundant in any particular place. Some of these species I did not consider sufficiently rare to merit further consideration, as they have since been found in localities not known to the authors of that *Flora*. In addition to the work of Loret and Barrandon I have relied for information concerning distribution on any relevant papers since published, on the Herbarium of the University of Montpellier, on botanists who have given me the benefit of unpublished information—particularly am I indebted to the late Prof. Ch. Flahault, Dr J. Braun-Blanquet, and Prof. J. Pavillard—and on my own excursions. Of the several hundred species mentioned I left out of further consideration sub-Mediterranean ones, and those of Boreal, Atlantic, and Sarmatic elements, which are represented among the rare species of Bas-Languedoc. I left aside all species known to be adventitious, of which there is a large number, and a few others which are almost certainly adventitious, being found exclusively on cultivated ground. After this elimination there remained the following eu-Mediterranean rare species, which constitute the subject of my enquiry.

#### A. *Species of calcareous rocks*

- |  |  |
|--|--|
| 1. <i>Asplenium glandulosum</i> Loisel. ( <i>A. Petrarcae</i> DC.)                 | 6. <i>Lavatera maritima</i> L.           |
| 2. <i>Oryzopsis caerulescens</i> (Desf.) Hack. ( <i>Milium caerulescens</i> Desf.) | 7. <i>Cachrys laevigata</i> Lamk.        |
| 3. <i>Melica minuta</i> L. ( <i>M. ramosa</i> Vill.)                               | 8. <i>Pimpinella tragium</i> Vill.       |
| 4. <i>Parietaria lusitanica</i> L.   | 9. <i>Ferula communis</i> L.             |
| 5. <i>Thelygonum cynocrambe</i> L.   | 10. <i>Teucrium flavum</i> L.            |
|  | 11. <i>Galium verticillatum</i> Danth.   |
|  | 12. <i>Phagnalon saxatile</i> (L.) Cass. |

#### B. *Species of calcareous garigue*

(Species marked with an obelus found also on siliceous garigue)

- |   |  |
|---|--|
| +13. <i>Andropogon hirtus</i> L.            | 21. <i>Ophrys bombyliflora</i> Link.   |
| 14. <i>Schismus barbatus</i> (L.) Thell.    | 22. <i>O. Speculum</i> Link.   |
| 15. <i>Asphodelus fistulosus</i> L.         | 23. <i>O. tenthredinifera</i> Willd.   |
| 16. <i>Gagea foliosa</i> R.Sch.             | 24. <i>Orchis longibracteata</i> Biv.  |
| 17. <i>Allium chamaemoly</i> L.             | 25. <i>Cytinus rubra</i> Pav. ( <i>Hypocistis rubra</i> Fourreau; <i>Cytinus Clusii</i> Nym; <i>C. hypocistis</i> L.; var. <i>kermesinus</i> Guss.), parasitic on <i>Cistus albidus</i> L. |
| 18. <i>Dipcadi scrobinum</i> (L.) Med.      | 26. <i>Buffonia perennis</i> Pourr.  |
| 19. <i>Narcissus dubius</i> Gn.             |  |
| *19 bis. <i>Sternbergia aetnensis</i> Guss. |  |
| 20. <i>Romulea ramiflora</i> Ten.           |  |

\* For convenience of reference I have retained the numeration employed in the list appended to the map.

<sup>1</sup> A eu-Mediterranean species is one which grows spontaneously—with perhaps rare exceptions—only within the Mediterranean region. A sub-Mediterranean species is one which, though more abundant in the Mediterranean region than elsewhere, apparently finding there the optimum of conditions it requires, is also found, though more rarely, outside the limits of the region. As there exists a difference of opinion on the limits of the Mediterranean region, I have commented on the question in *Les espèces survivantes tertiaires du Bas-Languedoc*, pp. 31, 32 and 37.

- 27.-*Paronychia argentea* Lamk.  
 28. *Velezia rigida* L.  
 29. *Delphinium staphisagria* L.  
 30. *Anagyris foetida* L.  
 †31. *Ulex parviflorus* Pourr.  
 32. *Ononis breviflora* DC.  
 33. *O. pubescens* L.  
 34. *Medicago coronata* Desv., Lam.  
 35. *M. leiocarpa* Benth.  
 36. *Melilotus italicus* (L.) Aschers and Graebn.  
 37. *Anthyllis tetraphylla* L. (*Physanthyllis tetraphylla* Boiss.)  
 38. *Astragalus glauus* L.  
 39. *A. narbonensis* Gn.  
 40. *A. pentaglottis* L. (*A. echinatus* Murr.)  
 41.-*Coronilla glauca* L.  
 42. *Hedysarum humile* L.  
 43. *H. spinosissimum* L. (*H. capitatum* L. and B. not Desf.)  
 44. *Lathyrus saxatilis* Vis. (*L. ciliatus* Guss.)  
 45. *Cneorum tricocum* L.  
 46. *Polygala rupestris* Pourr.  
 47. *Euphorbia polygalifolia* Boiss. and Reut.  
 48.-*E. sulcata* De Lens.  
 49.-*Helianthemum ledifolium* (L.) Willd.  
 50. *Fumana laevipes* (L.) Spach. (*Helianthemum laevipes* (L.) Willd.)  
 51. *Viola arborescens* L.  
 52.-*Passerina thymelaea* DC.  
 †53.-*Myrtus communis* L.  
 54.-*Bupleurum fruticosum* L.  
 †55. *Pimpinella peregrina* L.  
 56. *Seseli glaucum* L.  
 57. *Opopanax chironium* Koch (*Ferula sulcata* Desf., *Ferulaga sulcata* Desf., Koch.)  
 58. *Thapsia villosa* L.  
 59.-*Convolvulus lanuginosus* Desf.  
 60.-*Alkanna tinctoria* Tausch.  
 61.-*Sideritis hirsuta* L.  
 62. *Orobanche lavandulacea* Reichb. (*Phelypoea lavandulacea* F. Schultz)  
 63.-*Globularia alypum* L.  
 64. *Plantago albicans* L.  
 65. *Crucianella latifolia* L., Gn.  
 †66. *Galium maritimum* L.  
 67. *G. setaceum* Lamk.  
 68. *Scabiosa monspeliensis* Jacq. (*S. stellata* L. sensu auct. Languedoc)  
 69. *Inula helenioides* DC.  
 70.-*Santolina chamaecyparissus* L.  
 71. *Carduus leucographus* L. (*Tyrimnus leucographus* Cass.)  
 72. *Centaurea intybacea* Lamk.  
 73.-*Atractylis humilis* L.  
 †74.-*Lactuca tenerrima* Pourr.  
 75. *Zacintha verrucosa* Gaertn.

C. *Species of siliceous garigue*

- 76.-*Selaginella denticulata* (L.) LK.  
 77. *Airopsis tenella* (Cav.) Coss. (*Airopsis globosa* Desv.)  
 78. *Corynephorus articulatus* (L.) P.B.  
 79. *Carex oedipostyla* Duv.-Jouve  
 80. *Chaetonychia cymosa* (L.) Willk. (*Paronychia cymosa* Lamk.)  
 81. *Teesdalia lepidium* DC.  
 82.-*Lupinus hirsutus* L.  
 83.-*Trifolium purpureum* Loisel. (*T. Loiseleuri* Rouy)  
 84.-*Cistus crispus* L.  
 85.-*C. ladaniferus* L.  
 86. *C. populifolius* L.  
 87.-*Plantago bellardi* All.

D. *Halophytes and species of sandy places, particularly near the sea*

88. *Avellinia michelii* (Savi.) Parl.  
 89. *Rumex tingitanus* L.  
 90. *Loeflingia hispanica* L.  
 91. *Euphorbia pithyusa* L.  
 92. *E. terracina* L.  
 93. *Thymelaea hirsuta* (L.) Endl. (*Passerina hirsuta* L.)  
 94. *Bupleurum semicompositum* L.  
 95. *Statice confusa* Godr.  
 96. *S. diffusa* Pourr.  
 97. *S. duriuscula* Gir.  
 98. *S. ferulacea* L.  
 99. *S. psiloclada* Boiss.  
 100. *S. delicatula* Gir.  
 101. *S. tremolsii* Rouy.  
 102. *Limoniastrum monopetalum* (L.) Boiss.  
 103. *Elatinoides cirrhosa* (L.) Wettst. (*Linaria cirrhosa* Willd.)  
 104.-*Evax pygmaea* (L.) Brot. (*Evax umbellata* Gaertn.)  
 105. *Anacyclus radiatus* Loisel.

E. *Species of woods and prairies*

- 106.-*Carex olbiensis* Jord.  
 107. *Bellevia romana* Rehb. (*Hyacinthus romanus* L.)  
 108. *Iris xiphium* Ehrh.  
 109.-*Cytisus candicans* (L.) DC. (*Genista candicans* L.)  
 110. *C. triflorus* L'Hérit. (*Genista triflora* Rouy)  
 111. *Vicia pubescens* LK.  
 112. *Cyclamen balearicum* Willk.  
 113.-*C. repandum* Sibth. and Sm.

F. *Hygrophytes*

114. *Marsilia pubescens* Ten., Gren. and Godr.  
 115. *Pilularia minuta* DR.  
 116. *Isoetes duriae* Bory.  
 117. *I. setacea* Lamk.  
 118. *Althenia filiformis* F. Petit  
 119. *Polygonum romanum* Jacq.  
 120.-*Lotus coimbrensis* Willd. (*L. conimbriensis* Brot.)



- |  |                                      |
|--|--------------------------------------|
| 121. <i>Elatine macropoda</i> Guss.  | 124. <i>Heliotropium supinum</i> L.  |
| 122. <i>Peplis erecta</i> Req. ( <i>Lythrum Loiseleuri</i><br>Rouy and Cam.) | 125. <i>Pulicaria sicula</i> L.      |
| 123. <i>Oenanthe globulosa</i> L., Gn.                                       | 126. <i>Sonchus aquatilis</i> Pourr. |

*G. Species found mainly by the sides of roads*

- |   |  |
|---|--|
| 127. <i>Phalaris caerulea</i> Desf.                                       | 134. <i>Erodium chium</i> (Burm.) Willd.               |
| 128. <i>Aegilops biuncialis</i> Vis.                                      | 135. <i>Cerinthe major</i> L.                          |
| 129. <i>Spergularia atheniensis</i> Aschers.                              | 136. <i>Echium plantagineum</i> L.                     |
| 130. <i>S. diandra</i> Heldr. and Sart. ( <i>S. salsuginea</i><br>Fenzl.) | 137. <i>Cirsium echinatum</i> (Desf.) DC.              |
| 131. <i>Hypocotyle procumbens</i> L.                                      | 138. <i>Kentrophyllum caeruleum</i> Gren. and<br>Godr. |
| 132. <i>Trifolium spumosum</i> L.   | 139. <i>Scolymus maculatus</i> L.                      |
| 133. <i>Lathyrus clymenum</i> L.  |  |

None of these species has been found in fossil deposits of the neighbourhood, but other members of some of the genera have been discovered in fossil form. All of them have well-defined systematic positions, and none is subject to great variation. Some are extremely isolated systematically, e.g. *Cneorum tricoccon*, *Teesdalia lepidium*, *Anagyris foetida*, and *Thelygonum cynocrambe*. Feeble variability and well-defined systematic position are generally regarded, for example by Flahault, Lotsy and Maire, as characteristic of old-established species.

Most of our species are widely distributed throughout the Mediterranean basin, including the islands of the Mediterranean Sea (Balearics, etc.), which were separated from the continent in the Upper Miocene and Lower Pliocene (cf. Braun-Blanquet, 1926). This certainly confirms the evidence from the systematic position that we are dealing with species which are not of very recent origin. This wide distribution with its large gaps, this occurrence of species on the islands of the western Mediterranean, cannot be explained by dissemination under existing conditions.

The broken distribution within the area of special study seems likewise impossible of explanation in such a manner. In *Les espèces survivantes tertiaires du Bas-Languedoc* I have given a list of the various countries and of the Departments of France where the species are to be found, and in full detail their distribution within the area chosen for detailed study. Here it is not possible to give more than a few examples. It is very remarkable that *Marsilia pubescens* and *Pilularia minuta* are not found elsewhere in France than at Roquehaute (XII),<sup>1</sup> and *Sternbergia aetnensis* not elsewhere in France than at St Paul-et-Valmalle (XVIII). *Cyclamen balearicum* is found at Les Cambrettes (XVI); apart from this it is known only in the Balearic Islands. Several other species are found in only one locality within the area studied, e.g. *Iris Xyphium* at Roquehaute, *Ophrys Speculum* at Balaruc (XXII), and *Cyclamen repandum* at Pouzols, near Narbonne (V). *Lavatera maritima* occurs

<sup>1</sup> The numbers in brackets refer to the colonies as shown on the map, and are here inserted to give an idea of the approximate positions of the localities concerned to those unfamiliar with the territory. In each case the place mentioned is situated within the boundaries of the colony indicated.





at the Trou-de-Miège (XXVII), then about 50 miles away on the mountain of La Clape (VI), and again a few miles away at Feuilla (II), but nowhere else in the given area. Likewise *Hedysarum spinosissimum* is found at Agde (XII), then about 16 miles away near Nissan (IX), and about 10 miles further away near Capestang (VIII), but not elsewhere. *Cistus ladaniferus* is limited to the neighbourhood of St Chinian (VII), and that of Narbonne (V) about 20 miles away. These are but examples. Some species are found in two or three different localities, others in five or six, or even more, but for all the species there are great gaps in distribution which require explanation. I found also very striking instances of a few species not occurring in the area of special study, but existing to the east and west in more southern latitudes, which, as Flahault suggests, indicates probable survival from a more thermophile flora.

The ecology of the species has certainly strong bearing on the problem. In addition to the grouping into "species of calcareous rocks", etc., I classified them as far as possible according to their alliance and association, using the system given in Braun-Blanquet (1931). Here follows a brief summary of the species in the different alliances, each species being represented by its number in the list already given.

- (a) *Asplenion glandulosi*: 1, 2, 3, 4, 6, 7, 8, 9, 10, 12. 8 and 9 also belong to *Stipion calamagrostidis*.
- (b) *Ammophilion*: 89, 92.
- (c) *Hordeion murini* and *Chenopodion murali*: 129, 130, 134, 137.
- (d) *Ruppion maritimae*: 118.
- (e) *Staticion gallo-provincialis*: 93, 94, 95, 96, 97, 98, 99, 100, 101, 102.
- (f) *Isoetion*: 114, 115, 116, 117, 119, 120, 121, 122, 123, 125.
- (g) *Brachypodion phoenicoidis*: 23, 37, 55, 71, 105, 127, 132, 136, 139.
- (h) *Thero-Brachypodion*: 11, 14, 16, 17, 19, 19 *bis*, 20, 21, 22, 24, 27, 28, 32, 33, 34, 35, 36, 43, 44, 45, 48, 49, 58, 64, 68, 104.
- (i) *Aphyllanthion*: 42.
- (j) *Armerion juncei*: 60.
- (k) *Rosmarino-Ericion*: 31 (belongs also to (m)), 39, 40, 46, 50, 51, 52, 56, 59, 63, 70, 72 (belongs also to (a)), 73.
- (l) *Helianthemion guttati*: 77, 78, 80, 81, 83, 87, 88.
- (m) *Cistion ladanifer*: 79, 82, 84, 85, 86.
- (n) *Quercion ilicis*: 25, 30, 41, 53, 54, 106, 109, 110, 111, 112, 113.
- (o) *Species of uncertain association*: 5, 13, 15, 18, 26, 29, 38, 47, 57, 61, 62, 65, 66, 67, 69, 74, 75, 76, 90, 91, 103, 107, 108, 124, 126, 128, 131, 133, 135, 138.

The classification of the species in this way, together with a knowledge of the distribution of the different associations, establishes the fact that they are lacking from places which could, as far as we can judge, satisfy their ecological demands, though they are present in the neighbouring territory.

The means of dispersal is a matter of interest and importance. Active distribution by stolons and by explosive fruits does not concern us here, as it alone could not account for such large gaps. It is the means of passive distribution that demand further consideration. Water does not seem to play a role of much importance in the distribution of any of the species concerned. A few may be carried by men and animals, attached to clothing or fur. Adaptations in some fruits, e.g. those of *Hedysarum humile*, *H. spinosissimum*, and *Galium maritimum*, would facilitate this. But the situations in which these plants grow, with the exception of the few species found by the sides of roads, render it most improbable that this mode of dispersal has played an important part, particularly in the case of dispersal by man. Seeds of several of the species are carried by ants, but such means of dispersal could scarcely account for gaps of many miles. The case of the myrtle seems to be the only certain one of a fruit sought by birds for food, and birds may of course be responsible for carrying the seeds of the hygrophytes attached to mud on their feet. The wind is undoubtedly the most important agent in the distribution of the species under consideration. It could, perhaps, occasionally account for the disjointed distribution of some species. Some of the species are well adapted to dispersal by wind, e.g. *Scabiosa stellata* with its parachute of hairs, and members of the genera *Orchis* and *Ophrys* with their dust-like seeds. What is really striking, however, is the large number of species which have no known adaptation for dispersal, and the number which have conspicuously heavy seeds (or fruits, when they are the units of dispersal), e.g. *Anagyris foetida*, *Bupleurum fruticosum*, *Narcissus dubius*, *Romulea ramiflora*, and a number of others. How could species with such seeds owe their present distribution to dissemination under existing conditions? There is another interesting aspect of the problem. Why is it that some of the species, which have good means of dispersal, remain rare, when, as far as we can judge, the ecological conditions they demand are in their immediate vicinity? If we regard the species as relict species, their rarity in spite of good means of dispersal is more easily understandable: relict species—frequently at the limit of their geographical distribution—have a feeble power of extension. Defence is easier than conquest—they maintain their position, but cannot spread.

Mapping of the distribution of the species revealed the most significant fact of all. The species occur in colonies, a fact which gives immediate support to the hypothesis of survival. I tried several ways of indicating this distribution on a map of convenient scale and finally arrived at the present solution.<sup>1</sup> Where only one species occurs in any locality, or where a very few species occur together, the numbers indicating the species are written on the map. Where more than seven occur together, the group has been considered as a

<sup>1</sup> The map as reproduced here is on a very much smaller scale than that originally given in *Les espèces survivantes tertiaires du Bas-Languedoc*, wherefore the names and figures are less easy to read.

whole, designated as a colony, and marked by a rectangle. This is a slightly arbitrary delimitation, but the rectangle does represent approximately the limits of the area within which the members of the colony occur. It is in every case a more or less naturally delimited area—valley, gorge or hill. The species, members of the colony, are represented in the rectangles by dots, the total number of species in the colony being represented by the arabic numeral in or immediately beside the rectangle. The names of the species can be determined by the aid of the key at the side and foot of the map. The numbered list of species at the left-hand side corresponds to the list given in the text. These numbers are repeated along the top of the key under the map. The numbers of the colonies appear in Roman numerals at the left-hand side of the key. Reading the key horizontally one can determine the names of all the species in a colony. Reading it vertically one can determine the distribution in colonies of any species, though not its distribution in an isolated locality (or localities). In my earlier paper (1934) I have given classified lists of all localities within the given area where species are found, and this facilitates reference to the map. The map shows that the south of the area is markedly richer than the north in these rare species. Particularly rich are the colonies near Narbonne (V), with 72 species, La Nouvelle (III), with 60, La Clape (VI), with 43, and Agde (XII), with 40.

Further investigation of the conditions obtaining in the colonies showed several common characters. Firstly, the colonies occur largely in sheltered valleys, and on sunny southern slopes protected from north winds. Secondly, they occur mainly where the character of the vegetation is open, probably indicating initial stages of plant succession, and they are lacking in places where there is development of the climatic climax, which is here a forest. It would seem that these species have survived in open stages of plant succession, whereas in places showing development of the climatic climax they have been expelled by other species. This is reminiscent of the distribution of certain Alpine relict species at low altitudes on northern slopes in initial phases of plant succession. Thirdly, the colonies occur in places difficult of access to man, well removed from the destructive effect of cultivation and burning for pasture. Fourthly, I noticed that with rare and explicable exceptions none of the species under consideration occur on the coast between Sète and the Camargue, which region is new land, except at Maguelone, which is a small island of old volcanic rock. This led me to consider the nature of the substratum of the colonies. A fourth common characteristic was thus revealed, viz. that with rare exceptions the colonies occur on pre-Quaternary substrata. Of these common characters the first, that of situation in a favourable microclimate, is in accord with our theory of survival from a more thermophile flora. The second and third characters would obviously favour the maintenance of colonies of relict species. The fourth character, presence on pre-Quaternary substrata, is one which accords well with the interpretation of survival from

a more thermophile flora. The flora I would suggest is Tertiary, most probably Pliocene. It is known from fossil deposits that the Pliocene flora was very similar to that of the present day, but richer in heat-loving species. Even if we admit that dissemination under existing conditions could satisfactorily explain the present distribution of some species, such as the few growing near road-sides, or of a group such as the hygrophytes, how could one accept such an explanation for a colony? What chance distribution could bring together in these restricted areas such a collection of unrelated species? Briefly, the explanation I offer of the colonies—and no other explanation seems possible to me—is that they represent relict areas, residues of a more thermophile flora which existed in the Tertiary period, most probably in the Pliocene, and which in certain favourable positions has been able to survive the vicissitudes of climate of the Quaternary period.

The only exception to the occurrence of the colonies on pre-Quaternary substrata is on the Pleistocene in the south-east of the Department of Hérault, on land which was covered by a branch of the Rhone during the Pliocene. The colonies here are relatively poor in species. Further investigation reveals that most of the species are found in neighbouring places on a substratum of older rock, and, as several have good means of dispersal, we can postulate a migration, not necessarily recent. The species may have existed in intermediate places, and have been destroyed, probably by cultivation, as this is a much cultivated area. We must accordingly admit some slight modification of the explanation already offered of the existence of the colonies. All the places where we find examples of our rare species are not necessarily places of survival since the Tertiary. There have been, and still are migrations, which must in the past have been favoured by interglacial periods, by any changes in the direction of return to old conditions. For the rich colonies, however, the explanation of survival there since the Tertiary seems to me the most reasonable explanation of their existence. It is noteworthy that several of the richer colonies occupied an isolated position in the Tertiary period, which may have contributed to their present richness. Geological isolation tends to protect against invasions by other species capable of replacing previously established ones. In the Tertiary period, at least in the Miocene, the mountain of La Gardiole, to instance a rich colony, was an island, which was rejoined to the continent probably during the Pliocene. The same is true of the mountains of Sète and La Clape, also rich colonies, but their reunion with the continent was later.

As a matter of additional and kindred interest I compared the distribution of these rare eu-Mediterranean species with species which there is reason to believe are survivals from glacial periods. Both occur in colonies, but under different conditions of micro-climate; whereas the eu-Mediterranean species are on sheltered southern slopes, the others are largely on northern slopes and in other exposed positions. The rocks above St Guilhem in the valley of the

river Hérault are very interesting in this respect, for there we find both types of species, heat loving on the southern slope and the others on the northern.

In conclusion, I suggest that the results of my investigation strongly indicate that the rarity and disjointed distribution of a large number of species in Bas-Languedoc are chiefly due to changes in climate, which have led to the breaking up of previously continuous areas, and that the rare eu-Mediterranean species represent a residue of the more thermophile elements, now largely extinct in Bas-Languedoc, of the Pliocene flora.

## REFERENCES

- Allorge, P., Ambrose, A., Braun-Blanquet, J.** etc. "Histoire du peuplement de la Corse." *Bull. Soc. Sci. hist. nat. Corse*, 1926.
- Braun-Blanquet, J.** *L'origine et le développement des flores dans le Massif Central de France*. Paris and Zurich, 1923.
- Braun-Blanquet, J.** "Aperçu des groupements végétaux du Bas-Languedoc." *Station Intern. Géobot. Médit. et Alpine*, Montpellier, No. 16, 1931.
- Depape, G.** *Recherches sur la flore pliocène de la vallée du Rhône*. Paris, 1923.
- Depape, G.** "Le monde des plantes à l'apparition de l'homme en Europe occidentale. Flores récentes de France, des Pays-Bas, d'Angleterre." *Ann. Soc. Sci. Bruxelles*, sér. B, **48**, 1928.
- Dickinson, Olive.** "Les espèces survivantes tertiaires du Bas-Languedoc." *Station Intern. de Géobot. Médit. et Alpine*, Montpellier, No. 31, 1934.
- Flahault, Ch.** "Les progrès de la Géographie botanique depuis 1884, son état actuel, ses problèmes." *Progr. Rei bot. Jena*, 1906.
- Kieffer, M.** "Herborisations de Strobilberger à Montpellier en 1620." *Rev. Sci. Nat. Montpellier*, 1881.
- Laurent, L. and Marty, P.** *Flore pliocène des Cinérites des hautes vallées de la Petite-Rhue et de la Véronne, Cantal*. Marseilles, 1927.
- Loret, H. and Barrandon, A.** *Flore de Montpellier*. Montpellier, 1886.
- Lotsy, J. P.** *Evolution by means of hybridisation*. The Hague, 1916.
- Lotsy, J. P.** *Evolution considered in the light of hybridisation*. Canterbury College, N. Zealand, 1926.
- Maire, R.** "La distribution géographique de quelques plantes nordafricaines dans ses rapports avec la notion de l'espèce." *Fifth Intern. Congress, Cambridge*, 1930, 1931 (a).
- Maire, R.** "Contribution à l'étude de la flore de l'Afrique du Nord." *Bull. Soc. Hist. Nat. Afr. du Nord*, **22**, No. 8, 1931 (b).
- Martins, Ch.** "L'hiver de 1870-1871 dans le Jardin des Plantes de Montpellier et aux environs de cette ville." *Mém. Acad. Sci. Lett. Montpellier*, **7**, 1871.
- Planchon, G.** *Des modifications de la flore de Montpellier depuis le XVII<sup>e</sup> siècle jusqu'à nos jours*. Montpellier, 1864.



# PLANT SUCCESSION IN NORWEGIAN LAPLAND

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(*With Plates XIV–XVIII and four Figures in the Text*)

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## INTRODUCTION

NORWEGIAN Lapland is the district of Norway inhabited by the Lapps. As may be seen from the map (Fig. 1) it lies some distance north of the Arctic Circle ( $66^{\circ} 30' \text{ N. lat.}$ ) and, stretching to North Cape ( $71^{\circ} 10' \text{ N. lat.}$ ), constitutes the northernmost portion of continental Scandinavia. Ecological observations made on the vegetation during three visits totalling some six months, and including crossings of much of the country under both winter and summer conditions, are here summarised in the form of a general account of the main plant communities. These are arranged in successional series leading up to the climax,<sup>1</sup> but are purposely unencumbered by long descriptions and lists of the subsidiary plants, since most of the communities found were similar to those already well treated by Fries (1913), Du Rietz (1921 etc.), Nordhagen (1929) and others for the regions farther south, while some of them have actually been considered in a previous communication to this *Journal* (Leach and Polunin, 1932).

With the mean temperature almost everywhere in Norwegian Lapland exceeding  $10^{\circ}\text{C.}$  during July and August, when the sun may often be seen throughout the 24 hours, the growing season is sufficiently favourable for the development of quite luxuriant vegetation. Other environmental factors may,

<sup>1</sup> In the absence of long continued observations which would demonstrate the course of succession, the plant communities met with have merely, by comparison with the similar seres of more temperate regions, been interpreted according to the *probable* successional sequences.

however, have a profound effect upon plant growth, as is indicated by the great range of vegetational types to be seen within even a small area.

Compared with other regions of similar latitude the climate is greatly tempered by the proximity of the Gulf Stream—especially around the coasts, where the summer is fairly warm and the winter not at all cold, the mean annual temperature being 2 or 3°C. Inland the climate is much more continental in type, the winter being so long and so cold (more than 50° below zero Centigrade have been recorded) that although the summer is warmer than on the coast (the thermometer very occasionally rising above 30°C.) the mean annual temperature is almost always below zero. Unlike the coastal

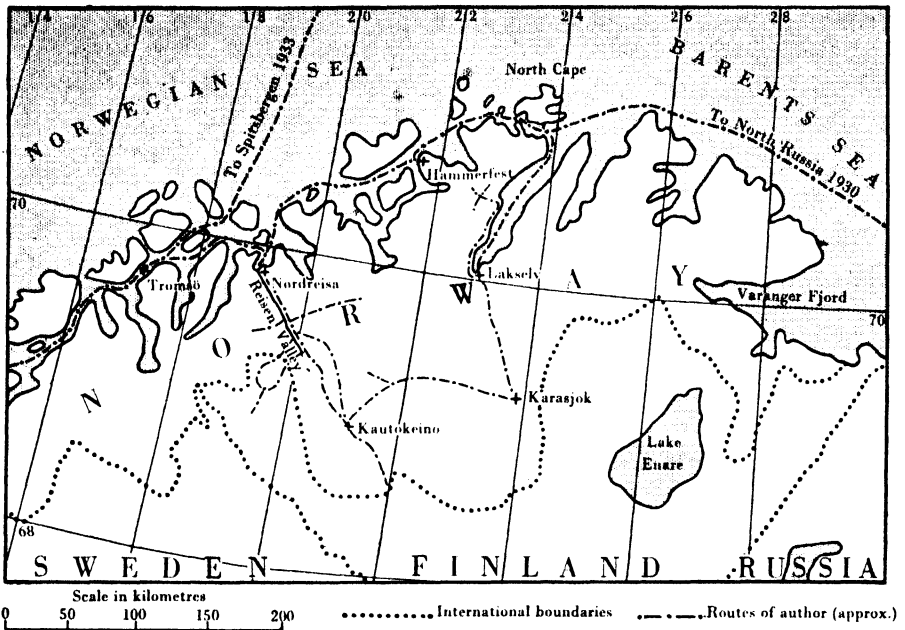


FIG. 1. Sketch map of Norwegian Lapland, showing author's routes

regions, frost can occur in any month of the year; the precipitation is also much lower than on the coast, but the snow lies longer (sometimes well into June).

This inland continental region consists of rather exposed plateau land which undulates, at least in contrast with the rugged mountainous coasts, rather gently around an altitude of 1000 ft. (304 m.). It constitutes most of the area of the mainland and has as its climax vegetation a low open woodland of scrubby birch, with *Betula odorata* the dominant and often the only tree (Pl. XIV, phot. 1 and Pl. XV, phot. 4). Various types of physiographic climax are also found, ranging from the true arctic-alpine vegetation of exposed uplands to quite luxuriant forests reminiscent of more southern climates in sheltered

valleys even in the interior, but particularly near the heads of the longer fjords which wander in far from the wind-swept ocean coast.

In the attainment of this climax there appear to be three main successional series, namely the *hydrosere* of lakes and ponds, the *psammosere* of dry sands, and the *lithosere* of exposed rock surfaces. Unlike the situation farther north or at high altitudes, where the usual course of succession is altered and the vegetation greatly reduced by the late melting of the snow, these main series of Norwegian Lapland have generally quite definite stages, many of which are essential. They are directly comparable with the seres of temperate regions and will now be outlined in some detail.

#### THE HYDROSERE

The hydrosere (see Fig. 2) consists of a series of eight more or less well-marked stages, starting with a submerged aquatic stage and continuing progressively through the floating leaf, reed swamp, moss colonisation and various shrub and tree stages to the climax.

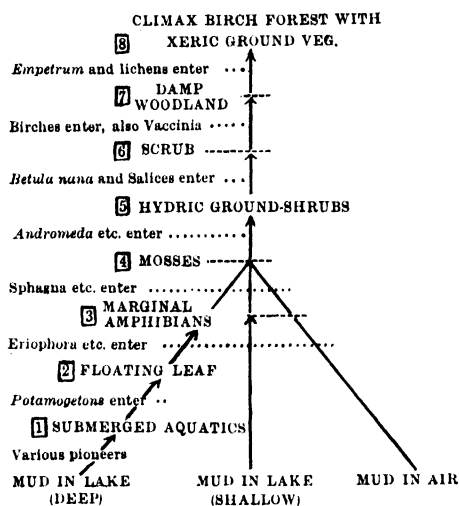


FIG. 2.

(1) *Submerged aquatics* constitute the first well-marked stage, apart from the fresh-water plankton which was not investigated. These submerged aquatics are best seen towards the margins of lakes and sluggish rivers, the most important types being Batrachian Ranunculi, aquatic mosses, Characeae and filamentous algae. Any of these may "fill" the water locally and form a well-marked "benthos" zone, while muddy beds in shallower water may support a miniature forest of *Hippuris vulgaris*, or more rarely of *Myriophyllum* sp.

(2) *Floating-leaf plants* often form a well-marked zone in the less exposed situations, especially near the edges of sluggish rivers. Species of *Potamogeton*

are the most universally important, as in England, although aquatic *Ranunculi* may form an aggressive mass locally.

(3) (a) *Marginal amphibians*, chiefly *Eriophorum*, *Carex* and *Equisetum* spp. (but sometimes including *Menyanthes trifoliata* and species of *Sparganium*), next form a reed swamp; and, by deposition of decaying matter and holding of silt, build up the soil level with comparative rapidity. Pl. XIV, phot. 2, shows the reed-swamp zone in a sheltered valley, where pines dominate the post-climax forest, and Pl. XV, phot. 3, shows a lake in a still more sheltered situation where conspicuous broad leaves of *Menyanthes* form a marked feature of the truly amphibian zone. In some of these lakes in sheltered valleys, large *Carices* have been observed colonising mud under water a metre or more deep.

(b) An alternative mode of initiation of the hydrosere, without the earlier aquatic stages, is seen in many glacial lakes where the water is shallow and liable to recede in level as the summer draws on. Such lakes are very numerous on parts of the plateau of Central Finmark (North Norwegian Lapland) and frequently have amphibian *Carices* and *Eriophora* as the first colonists of their beds. These beds are only slightly shelving and have a greater or lesser deposit of silt in which the colonists root—sometimes growing far out but generally (in these exposed plateau areas) not where the water is more than a foot (30 cm.) deep in summer. If the level of the lake falls in summer so as to leave deep wet mud with its surface exposed to the air, there may be much *Scirpus caespitosus* entering between the taller reed-swamp plants before the whole becomes overgrown with the *Sphagna* and other mosses which initiate the next stage (No. 4) in the sere.

(c) Although it certainly does not concern the colonisation of open water and possibly does not belong to a prisere at all, yet another mode of initiation was seen in some badly drained upland areas where lowlying patches of very wet mud alternated with raised tussocks of *Sphagna* and other mosses. The mud was deep and acid, doubtless acquiring much of the latter property as a result of drainage from the *Sphagnum* tussocks, and it was almost always occupied by an open community of mixed *Eriophorum*, *Carex* spp. and *Scirpus caespitosus* before the mosses extended over it—an extension which seems to be very slow in these exposed upland areas, often taking place only after colonisation by small ground-shrubs such as *Andromeda polifolia*. The wettest areas are those facing north and presumably having an abundant snow covering in winter and a growing season much shortened by its late melting.

(4) *Sphagna* and other tussock-forming mosses constitute the next stage. Although in Arctic Europe the writer has noted *Sphagna* as being of some ecological importance in sheltered habitats almost as far north as the 80th parallel of latitude in Spitsbergen, and in Arctic America as far north as the 74th parallel on Devon Island, yet on the general plateau of Norwegian Lapland they seem already to be nearing the northernmost limit at which they can be really aggressive in exposed areas. For on this plateau they do not generally

extend out laterally over deep water to form the floating masses which are so well known farther south, and which may also be observed in the most sheltered valleys of Norwegian Lapland (see Pl. XV, phot. 3). However, on the plateau *Sphagna* still seem able to colonise any relatively stable wet mud, by slow lateral growth from tussocks or a bank, even as they can colonise a reed swamp—and thus all the stages that have gone before are given a merely indefinite or *proseral*<sup>1</sup> significance.

Fig. 2 (p. 374) shows the relationships of the stages of the hydrosere, the numbers being those of the present description. While one or another of the initial stages noted is generally evident, it is not really essential—since the mosses can colonise barren wet mud and, at least in sheltered valleys, open water. But on the other hand the *autogenic main sere*<sup>1</sup> seems always to continue through a stage of colonisation by slow-growing, tussocky *Sphagnum* sp. or spp. (usually aided by other mosses and bound by the roots of Cyperaceae), and thus the moss stage (4) is the first phase of the hydrosere that is essential and universal. It also constitutes a big step in the progressive drying out of the habitat, for the mosses grow up to such a height—generally in variously sized and spaced, rounded tussocks—that water is no longer so easily raised by capillarity to supply the living shoots, and the resulting dry hummocks are colonised by *Polytricha* and *Cladoniae*. Often there may be regression, even to a crustaceous lichen stage, on the tops of the higher hummocks, where the surface is parched by the sun in summer.

(5) *Ground-shrubs* form the next stage. Of these *Andromeda polifolia* and *Rubus Chamaemorus* are the most hygrophytic and the first to enter, generally followed by the taller *Ledum palustre* and *Salices*, which help greatly to dry out the habitat, both by building up the surface and by making greater demands on the water supply. The *Sphagna* and any other relatively hygrophytic mosses are by this time generally dead towards the tops of the tussocks, although the sides may be alive and actively extending to cover the area.

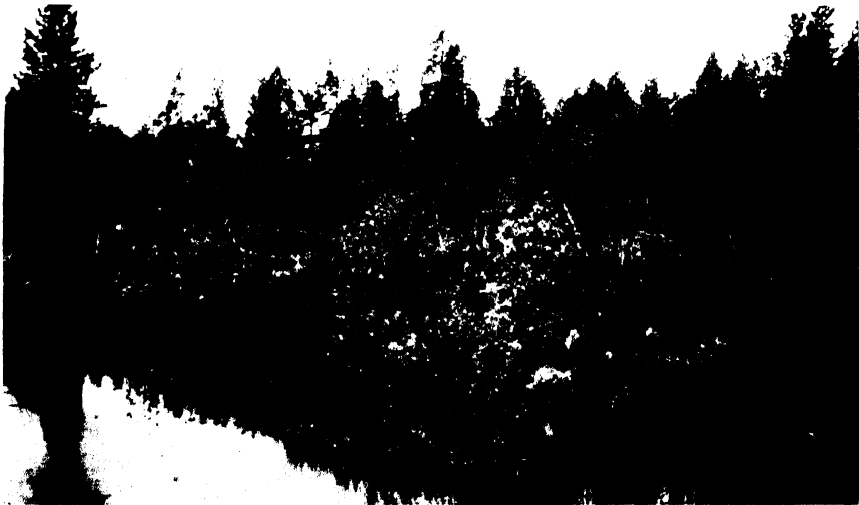
(6) *Betula nana scrub with Salices* is the next stage, and persists as an altitudinal climax above the tree limit (Pl. XVII, phot. 11). Its incidence is consequent upon the improvement of the habitat by the progressive desiccation and death of the *Sphagna*, and its taller bushes in their turn kill out the water- and light-demanding *Andromeda* and other ground-shrubs. The scrub is a thick tangle, in most places limited to about 2 ft. in height by the depth of the snow-covering in winter. In sheltered valleys or depressions where the snow becomes deeply drifted the scrub may be much taller and consist largely or entirely of *Salices*, which slowly open out as regeneration fails with further drying of the soil, and allow of colonisation by birches which assist in the final killing out of the scrub by competition—except that some *Betula nana* may persist in places as an upper shrub layer in the next stage.

<sup>1</sup> See footnote on p. 196 of "The Vegetation of Akpatok Island. Part II." This JOURNAL, 23, 1935.





Phot. 1. Climax open birch woodland; trees 3-4 m. high. On south-facing slopes and porous soils the dark heathy ground vegetation is much interrupted by dry patches of light-coloured lichens.



Phot. 2. Hydrosere in sheltered valley. Stages visible are: marginal amphibians (above water in foreground), moss-compacted reedswamp, *Salix* scrub (poorly marked, light-coloured zone in middle distance), birch-alder thicket and pine forest post-climax.

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(7) *Damper type of birchwood.* This in favourable situations where they can grow, may have associated small alders, rowans and aspens, sometimes forming an almost closed canopy. On the ground are low shrubs (especially *Vaccinium uliginosum* which is tolerant of great extremes in water conditions and is therefore almost ubiquitous), herbs and grasses, the community passing to the next stage on further drying of the ground.

(8) *Climax birch forest.* This covers most areas that are not too exposed. The trees of the more mature types are in open formation (Pl. XIV, phot. 1 and Pl. XV, phot. 4), generally small (3–4 m. high) and shrubby, and on porous soils often evenly spaced as a result of root competition.<sup>1</sup> The ground vegetation consists most typically of xeric under-shrubs, chiefly *Empetrum hermaphroditum*,<sup>2</sup> but including *Vaccinium Vitis-idaea* and *V. Myrtillus* and often *Arctostaphylos Uva-ursi* and *Phyllodoce coerulea*. The continuity of the ground-shrubs is frequently much interrupted by still drier areas of light-coloured lichens, principally those tall *Cladoniae* which constitute the so-called “reindeer-moss”. The herbs at best are very few indeed—generally no more than a tuft of *Festuca ovina* or *Deschampsia flexuosa* every few metres, with here and there a flowering axis of *Solidago Virgaurea* or *Epilobium angustifolium*, or more rarely of *Pedicularis lapponica* or *Pyrola* sp. Finally in the shade of the larger birches there may sometimes be a little dried-up *Cornus suecica* or *Trientalis europaea*.

#### THE PSAMMOSERE

This generally starts with the invasion of bare sand by plants which are already of some size and complexity (often rhizomatous ground-shrubs) and so has relatively few really essential stages. (Nevertheless, we frequently see in the psammosere, as we did in the hydrosere, variable and unnecessary proseral stages (see Fig. 3) before the initiation of the main sere whose every stage is definite and essential for incidence of the next.)

The psammosere is quite distinct from the lithosere; not only do these two main types of xerosere differ markedly in their plant colonists, as of course they do in habitat type, but they never become quite alike even in their climax stages, although both rise to more or less complete exploitation of the ground by the trees of their respective forests.

(1) *Elymus arenarius*, the well-known sand-binding lyme grass, is to be seen at its usual work by the sea at the heads of fjords (Pl. XVII, phot. 12). On the plateau *Elymus* is rare and the “blow-outs” of dry sand are often first bound by mosses, chiefly *Polytricha*. The most important types in this

<sup>1</sup> In sheltered valleys the trees may be very much larger, sometimes exceeding a metre in circumference (breast high) and 14 m. in height.

<sup>2</sup> With the exception of occasional lowland plants which are properly referable to *Empetrum nigrum*, all the *Empetrum* in Norwegian Lapland seems to belong to the monocious giant tetraploid *E. hermaphroditum* (Lge.) Hagerup. No distinction was recognised by previous writers on Norwegian Lapland, all the *Empetrum* in these regions being called *E. nigrum* L. (cf. **Norman**, 1894; **Leach and Polunin**, 1932).



connection are *Polytrichum juniperinum* and *P. piliferum*, which, like *Elymus* on a larger scale, are able to grow through successive layers of sand deposited to cover them, keeping the new surface stabilised by their closely clustered wiry axes (cf. Leach, 1931). Even if the apices project hardly at all above the surface, their binding influence nevertheless allows the sand to conserve water much better.

(2) *Festuca ovina* is generally the next colonist between the tufts of the larger *Elymus*, or, on the inland sand where this is usually absent, among the mosses. Sometimes *Festuca* enters alone as a pioneer, but as such is liable to be destroyed by drought or movement of the sand.

(3) *Ground-shrubs*, chiefly *Empetrum*<sup>1</sup> and *Arctostaphylos Uva-ursi* (or in upland regions often *A. alpina*<sup>2</sup>), which spread rapidly by rhizomatous growth in the absence of competition, form the next stage. Since they are quite frequently to be observed colonising bare sand—at least from the edges of areas already stabilised by higher vegetation—which apparently had no previous

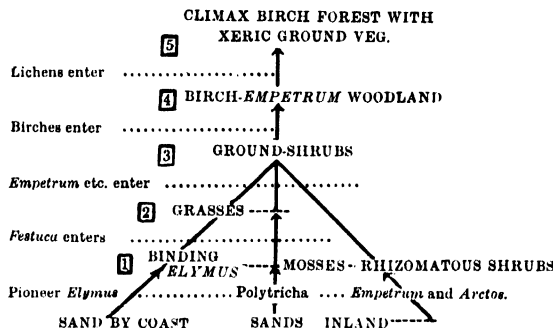


FIG. 3.

plants to give humus *in situ*, these rhizomatous ground-shrubs may be considered as the first really essential stage in the psammosere. By lateral extension (which is probably quite rapid, at least when accompanied or preceded by mosses) single plants often form patches as much as 2 m. in diameter. They bind the sand almost perfectly and form a mulch, which allows it to conserve moisture, so that the less xeromorphic *Vaccinia* can enter.

(4) *Birches* appear in the heath resulting from such colonisation when there is a sufficient deposit of humus to hold water near the surface. Sometimes they establish themselves from seeds, or they may enter as suckers from nearby trees; but such colonisation as was observed was only in the most luxuriant patches of ground-shrubs (especially tall and green *Empetrum*) and this fact, considering the dryness of the forest behind, may be taken as an indication of the nature of the last stage in the establishment of the climax.

(5) *Gradual opening out of the ground heath* as lichens enter and dominate many areas.

<sup>1</sup> See footnote on p. 377.

<sup>2</sup> Cf. Akpatok Island (Polunin, 1934).





Phot. 3. Lakeside in sheltered valley showing marginal amphibian zone (the broad leaves of *Menyanthes* are conspicuous) and floating islands of *Sphagnum* supporting *Eriophorum* and *Carex* spp.



Phot. 4. Poor birch forest on upper slopes of river valley under deep snow in winter. Open pine forest visible in valley bottom, particularly on the left.

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On the porous sands which cover many parts of the country, little of the water from the melting snow is retained near the surface, and the insolation being extreme and the supply from summer precipitation very precarious, it is probably the extra demands made on the water supply by the birch trees that leads to this regression to lichens. Certainly *Empetrum* grows greenest and best on the edges of the sandy areas where there are few or no birch roots.

With the severe root competition resulting from the insufficiency of available water, the trees become bushy and very evenly spaced. Most typically they are about 5–8 m. apart and no more than 4 m. high, and consist of a number of slender poles coming from each old stool, while the dark ground-shrub patches become in time so definitely delimited from the lichen areas that their respective soils may show different profiles and pH relationships. In the very driest regions, with the soil of coarse sand that cannot retain water and the slope southerly so that the surface becomes parched by the sun, the trees are still farther apart and the ground-shrubs (generally *Empetrum* with a little *Vaccinium Vitis-idaea*) may become limited to small areas shaded by them (Leach and Polunin, 1932, Pl. XXIX, phot. 16). Forbs and even grasses may be absent from such a patchwork, the surface, especially of the light-coloured lichen areas, being parched and crumbly, crackling under foot in summer. Nevertheless we may be reconciled with the theoretical conception of increasing moisture of the xerosere, for it is the birch trees dominating the formation which matter, not the ground flora and its appearance.

#### THE LITHOSERE

This, at least in its earlier stages, must be exceedingly slow (cf. Cooper, 1928). It starts (Fig. 4) with the colonisation of bare rock surfaces by small and generally slow-growing, primitive plants such as Cyanophyceae or crustaceous lichens, continuing progressively through higher lichen and moss stages to herbs, shrubs, and finally to the climax woodland with ground-shrubs subdominant. Once again the earlier stages that are usually seen appear to be non-essential.

(1) *Blue-green algae* are typically the pioneers, forming a more or less continuous investment of a powdery consistency in any moisture-retaining crevice or smaller depression in the rock, and on the undersides of boulders. In both of these situations the shelter and water conditions are much more favourable than on the exposed rock surface, and the light being sufficient for photosynthesis, growth and extension of the colony proceed in the absence of competition. These colonies are certainly to be considered as merely proseral, in that they are local and not essential in the initiation of the autogenic main sere on such substrata—a fact which is shown by the absence of Cyanophyceae from the upper surfaces of rocks in dry situations, although these same surfaces may be plentifully colonised by crustaceous lichens or often by other types of higher life form.

(2) *Crustaceous lichens*, especially Lecideae, are the pioneers on dry exposed rock or boulder surfaces as opposed to crevices and depressions, whether they are entirely covered with snow in winter or not. Succession on such rock faces in the Arctic must be extraordinarily slow, especially if the rock is particularly hard: indeed its advance depends almost entirely upon the activity of the chomophytic (i.e. crevice) communities. We frequently have lichens coming in as a second stage after the Cyanophyceae, which in time are ousted; and although the growth of crustaceous lichens is notoriously slow, even in places where they can grow at their best, their activity must in time have some effect upon even the hardest rock, causing disintegration by physical and chemical means, and depositing humus, so that with the weathering of the parent rock a little soil becomes accumulated.

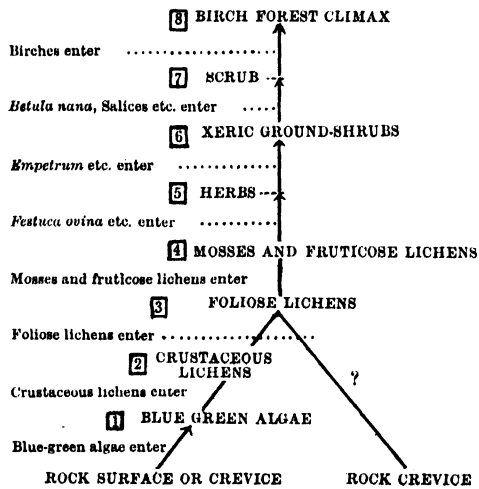


FIG. 4.

(3) *Foliose lichens*, especially Gyrophorae, usually enter next. They overshadow and in time exterminate any crustaceous types which may have formed a nidus for their ecesis—although in some cases they seem able to colonise even a bare rock surface, especially if it is rough. This entry of foliose lichens produces a considerable change: being often large they are able to collect and accumulate dust, rock particles and humus much more rapidly than did the less bulky crustaceous forms, which hardly project at all above the surface of the rock.

(4) *Mosses and fruticose lichens* enter next. Being still higher in both life form and stature, they overtop and oust the previous types and quickly get to work weathering the rock, accumulating dust and forming soil, which is held often to a thickness of several centimetres in their close tussocks. But again we see telescoping: for although more careful study (especially over long periods of time) is necessary, there is abundant suggestion of certain mosses

being able to colonise alone the bare rock of slight crevices, even though the surface around is uncolonised or supports no more than a few crustaceous lichens. If the autogenic main sere can start thus without them, and moreover can start on bare rock with a stage above them, this would give but a proseral significance to all the previous stages, and point to their being non-essential as humus producers and soil accumulators. In any case it is almost entirely the activity of the larger mosses, and of the fruticose lichens such as *Cladonia* spp. and *Stereocaulon paschale* which may grow upon them, that produces a habitat suitable for higher plants.

(5) *Herbs*. This stage in the lithosere is often but poorly marked in the Arctic. Thus on exposed areas of the plateau of Norwegian Lapland it is generally represented only by one or two grasses, particularly by *Festuca ovina*. On rocks and boulders in sheltered forest areas, however, the herb stage may be relatively well marked, with Cruciferous annuals, *Solidago Virgaurea*, *Cornus suecica* and *Trientalis europaea* in evidence, as well as *Festucæ* and other grasses; while in the most sheltered and humid valleys this stage is almost as important as any other, being represented by a sward of forbs and grasses just as in temperate regions.

(6) *Xeric ground-shrubs*, especially *Empetrum*, are however generally much more important than herbs in the Lapland lithosere. With the water and nutrition difficulties on rocks, and with the frequent absence of any blanket of snow in winter, these ground-shrubs are of stunted growth and reduced form except where they grow in crevices, which they may fill rapidly. Such crevice or chomophytic communities, however small they may be in extent, are especially important in succession; although they introduce telescoping, being often well vegetated when the rock around them is bare, they can go through identical pioneer stages (except perhaps for the greater importance of Cyanophyceae at first) and must not be considered as anomalous seral types but mere localised areas of different exposure, microclimate and water conditions in which succession has taken place more rapidly, the conditions for ecesis and growth being much more favourable.

The "crevice effect" is most marked on exposed areas such as mountain tops, and is largely bound up with the question of relative shelter—not only from almost continuous winds in summer but also in winter, when ice fills or snow covers the crevices, and the mass of vegetation and humous soil in them is frozen solid and so protected from desiccation. Where the exposed rock surface around is bare of snow in winter, so that it still remains barren except for a few inconspicuous crustaceous lichens, the crevice communities may be maintained indefinitely as sublimaxes somewhat deflected from the main sere. But elsewhere from the crevices or from other areas (or, in the case of small boulders in favourably sheltered localities, from the heath around), ground-shrubs may extend quite quickly over a bare rock surface. Where they do this on hard rocks that remain smooth and little weathered, the resulting peaty

mass of closely woven roots and humus may be removed intact, leaving the rock surface quite clean, and one remarkable case was observed where this had been done by wind!

Except in places of humid atmosphere where mosses grow luxuriantly and soon provide a nidus for ecesis of higher types, boulders which have not been colonised by extension of the heath from surrounding areas are generally covered with a cap of higher vegetation only if they have somewhere on the surface a niche which helped the original ground-shrub colonist to attain ecesis. Certainly extension from the faster developing communities of crevices is very important in plant succession on the harder types of rock. In bouldery moraines (if conditions are not too dry) the caps of vegetation may join from boulder to boulder, in time making a continuous carpet, which comes to show less and less the undulations due to the underlying boulders, till finally after a very long period the peaty soil may be thick and the surface smooth. Then the only indications of the nature of the substratum, and of the sere which led to the present climax, are occasional holes still left between some of the larger boulders, whose sides are thus exposed, clean and almost unchanged. The humous soil is so interwoven with roots that it does not crumble and fall to fill these spaces; the gaps persist, or become bridged by a thin carpet of massed roots and ground vegetation, constituting perfect death-traps.

On the other hand, on screes of large jagged rocks the conditions are very dry, and higher plants generally exist only in the depressions between adjacent blocks, where cryptogams grow best and where humus accumulates and forms a nidus. Only when the level is built up considerably and the depressions are largely filled, will the tops of the rocks be covered with higher vegetation (Pl. XVI, phot. 5 shows the last projecting rocks of a scree being covered by *Empetrum*, chiefly on the sheltered (left-hand) side).

Although *Empetrum* is the most universally important of the ground-shrub colonists, *Arctostaphylos alpina*, which can spread still more rapidly by its rhizomatous growth, may replace it in some of the most exposed situations, while the other extreme of damper birch forest may have its boulders colonised chiefly by *Vaccinium Myrtillus*.

(7) *A later shrub stage*, represented by such larger types as *Juniperus*, *Betula nana* and hairy, white-leaved *Salices* such as *Salix lapponum* and *S. lanata* may, with the increased water-retaining capacity of an ever-thickening humous soil, in time enter and dominate the ground-shrub stage of the normal lithosere. This later "scrub" stage, including as it does many rampant and deciduous bushes, proceeds to build up the soil still more rapidly, until the area is ready for colonisation by birches.

(8) *A birch forest climax* is reached in time. On rocks this climax has a closer canopy and finer trees than the type on porous sands, and, especially on north-facing slopes which are not too highly insolated, has a more luxuriant ground vegetation often dominated by *Vaccinia* (particularly *Vaccinium Myr-*



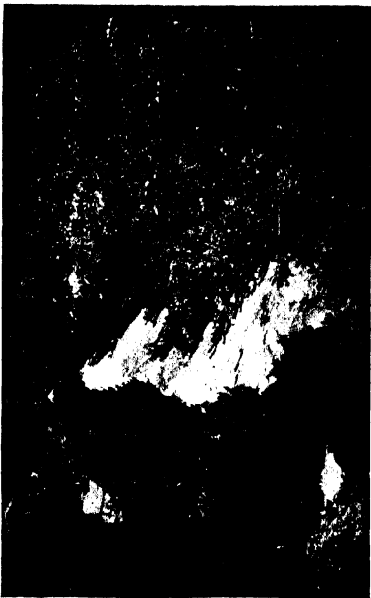




Phot. 6. Reindeer resting after feeding on dwarf vegetation of exposed hilltop, the first area bared of snow in early summer.



Phot. 8. Later stage of Phot. 7. Sand bound by grasses, with willows in background.



Phot. 5. Late stage in colonisation of rough scree. *Empetrum* almost continuous, but poor on windward (right-hand) side of projecting rock.



Phot. 7. Prostrate *Equisetum arvense* and larger grasses colonising river-deposited sand, damp below surface.

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*tillus*) and including many herbs. The chief of these are *Epilobium angustifolium*, *Cornus suecica*, *Trientalis europaea* and *Deschampsia flexuosa*, whereas on sandy areas herbs are generally absent or confined to very occasional dwarfed plants of *Festuca ovina*, *Calamagrostis* sp. and *Solidago Virgaurea*, which also occur in the more luxuriant rocky forest now under consideration. This difference seems to result from the better drainage on the poorer sands. Both types belong to the xerosere, and the dampest and most luxuriant stage which can be reached must be recognised as the true climax. This makes the birch forest of the psammosere with its dry *Empetrum*-lichen ground vegetation an edaphic climax, really a subclimax if we consider Norwegian Lapland as a whole; or perhaps the two types of birch forest are best considered as different communities of the same birch forest xerosere, the psammo- and lithoseres being kept distinct to the end.

#### THE MESOSERE

In considering the dynamic ecology of many regions, at least in the Arctic, it seems necessary to distinguish a *mesosere*, or succession starting with the colonisation of suitable bare areas neither by hydrophytes nor by extreme xerophytes but, instead, by some of the more mesophytic plants existing in the region. A mesosere may also be defined as a succession starting on an area which is devoid of plants but damp—with a lasting supply of ground water at least until the plants have changed the conditions. Generally it concerns only a small area of the region under consideration, but as a concept it is none the less necessary, although the mesosere itself varies with the type of bare area to be colonised. It varies also in the later course of the sere, which however tends almost always towards more mesophytic conditions before reaching the climax.

One example of a mesosere has already been described, namely the relatively hydric succession which started with the colonisation of areas of wet mud in upland regions by Carices and Eriophora which were later followed by Sphagna. Because of its great similarity with the true hydrosere, both in the hydromorphic nature of its colonists and in the detail of its later stages, it was best considered with the hydrosere proper.

Another type, which is rarely encountered, has a landslide as the agent of nudation. The landslide in the examples seen appeared to have been started by the action of water percolating from melting snow, and the same source keeps the bared soil wet and favourable for rapid colonisation by mesophytic herbs.

A third type of mesosere, which is of much greater importance at higher latitudes than Lapland, is that developing in habitats kept wet by late-melting snow whose water remains *in situ*. A zoned series of subclimaxes results, the determining factor being the successively more and more shortened growing season as the centre of the patch is approached; but since the outer

zones generally dry off quickly after the snow has left them, and the innermost ones which belonged to the mesosere are kept at or near the pioneer stage, this type of area is better considered separately under "snow covering". However the incidence of a few hygrophytic-microthermic phanerogams in places shows that successional advances can take place, and shows moreover which way the mesosere is tending.

Finally there is the mesosere which starts with the colonisation of banks of river-deposited sands or finer silt where water can be reached by the roots of vascular plants beneath the surface. The pioneers are very often little rhizomatous plants of *Equisetum arvense*, or sometimes of grasses. Pl. XVI, phot. 7 shows a somewhat later stage where these colonists have multiplied, for they are able to grow up through the layer of sand deposited annually by the spring-time flood of snow water; and Pl. XVI, phot. 8 shows the final stabilisation of the sand by large grasses and herbs (and on the surface between them, by mosses) which kill out the first colonists and allow the entry of willows (seen in the background of Pl. XVI, phot. 8, although most of those on the left are growing on a sheltered bank beyond) and later of birches. By this time the very course of the river may have been altered, the banks of sand or silt getting higher and higher as more material is deposited between the axes of the binding plants until the water has to go around some other way.

Where the bed is coarse and gravelly the first colonist of any importance is often *Silene acaulis*, whose close tussocks grow until they may be as much as a metre in diameter and nearly  $\frac{1}{2}$  m. high, so that willows can attain ecesis in their shelter. Thus again the area may in time become continuous with the adjacent climax regions if the water has found another course; and indeed this often happens in the valleys of Norwegian Lapland where conditions are favourable for the strong growth of the necessary plant colonists.

#### THE PINE FOREST POST-CLIMAX

In some of the more favourable and sheltered valleys, particularly towards sea level near the heads of the fjords coming from the Atlantic coast on the west, *Pinus silvestris* (chiefly the tall and tapering *forma lapponica* seen in the photographs) is able to grow and dominate the birches, whether their forest belonged to the hydrosere, psammosere, lithosere or mesosere sequence. The result is generally a rather poor and open pine forest (Pl. XVII, phot. 9) with associated birches (although the individual pine trees in girth and height are often comparable with those of Central Europe<sup>1</sup>) and on the ground a heathy investment of *Empetrum* and *Vaccinia*—with an abundance of lichens if the situation is dry, or of mosses with some herbs if it is relatively moist. Not only has cutting of the pines and other human interference been considerable in places, but regeneration of the species almost all over Lapland is

<sup>1</sup> For example, one of the greatest pines the writer has ever seen grows in Reisen Valley at a latitude of nearly 70° N. It is over 3 m. in circumference breast high.

very uncertain, the distribution itself being apparently limited by the necessity of recurrence within the life period of three consecutive summers sufficiently warm and sunny for pollination and the ripening of the seed, or possibly of one that is exceptionally hot.

The pine forest in the more sheltered valleys constitutes a post-climax if we consider the region as a whole; indeed the rest of the vegetation in these valleys at the heads of the larger fjords is incomparably more luxuriant than on the general plateau, including some entirely different types of community. But beyond calling attention to the examples shown in photos. 2, 3 and 14, these will not be described here since they are relatively unimportant considering the area as a whole.

It is interesting to note that the recovery of closed vegetation on small artificially denuded areas is quite rapid in these sheltered valleys, although this may only be where the soil is mixed with some humus. Thus soil laid bare of all vegetation and litter early in the summer in Reisen Valley (see map, Fig. 1) is soon colonised by mosses, chiefly *Funaria* spp., so that by the first autumn these cover about half the area in the shade but much less where the surface is parched by the sun. A few angiosperm seedlings may appear the first year. In the second year the shaded parts become completely covered with a continuous investment of mosses and many angiosperm seedlings and shoots of *Equisetum arvense*,<sup>1</sup> but the only plants seen to flower were *Festuca ovina* and *Rumex acetosella*. In shadeless places the mosses now cover about half the area, making the soil far more retentive of water, so that in the third year the whole becomes completely carpeted over. The plots now bear seedlings or larger (often flowering) plants of the majority of the types from the pastured areas around.

#### BIOTIC DISTURBANCE AND THE PASTURING "SUB-CLIMAX"

It seems probable that few areas even of the vast uninhabited plateau regions of Norwegian Lapland are entirely free from the biotic factor introduced by man or his pasturing animals, particularly reindeer. Thus many of the areas now dominated by birches, in valleys vegetated elsewhere by pine forest, bear evidence of the pines having been cut extensively, although other birch areas existing in damp depressions represent true birch societies (Polunin, 1931). Birches as well as pines are often cut for firewood or the building of huts. Using a long caravan of reindeer sledges, a single Lapp can take all the wood from several acres in a day or two, the trees are so sparse, and with growth very slow whole areas around the settlements have been deforested.

Although most of the plateau is uninhabited, the Lapps may wander almost anywhere with their herds of reindeer, and Pl. XVI, phot. 6 shows how these creatures flock to the first patches left bare when the snow melts in spring, eating and trampling the lichens so heavily that regeneration may

<sup>1</sup> I.e. in the case of the chief shaded experimental plot that was made and watched.

take 20 or 30 years—sometimes almost as long as the regrowth of a forest after cutting. Indeed there is little doubt that the larger arborescent species of *Cladonia* and *Stereocaulon*, on which the reindeer mainly subsist in winter, were once far more abundant than they are to-day, although they still form dense “reindeer-moss” communities in places.

Even in the upland regions above the birch limit, pasturing may be of considerable importance. For in summer the reindeer repair either to the coast or to these windy heights to get away from the worst of the mosquito plague, and at this season will eat almost anything. Thus large areas of the treeless upland plains bordering the great Porsanger Fjord which opens into the Arctic Ocean are dominated not by one of the usual upland heath communities but by grasses (particularly *Festuca ovina* as in Britain) or sedges which are able to withstand heavy grazing and trampling. Any herbs or ground-shrubs which persist are nibbled off close to the ground.

In all these cases the biotic factor is important in modifying the vegetation, generally producing a sub-climax—which may be maintained indefinitely or in other cases may change appreciably along a line of progression which does not form part of the usual sere and so exemplifies “deflected succession” (Godwin and Tansley, 1929). This is best seen where the biotic (primarily anthropoeic) factor is most intense and lasting, namely in the settlements and around the occasional huts set in pastured clearings which occur here and there along the larger rivers. The less nomadic Lapps living here generally own a few cows, ponies, goats or sheep and these may be kept in fenced-in clearings for the summer. Intensive grazing year after year in the same small enclosure results in the appearance of a pasturing “subclimax”—really an example of deflected succession since it becomes in time a grassy meadow with a thick turf quite unlike anything seen in any of the normal seres of the region. This phenomenon is of course commonly to be observed in almost all inhabited parts of the globe.

#### ALTITUDE, ASPECT, EXPOSURE AND SNOW-COVERING

It is believed that all the major vegetational types to be seen in Norwegian Lapland have been considered and put into their correct places in the scheme given above. But if we are to embrace everything within the area we must mention a few more minor communities which are developed locally wherever one or more of a certain group of environmental factors become particularly intense. These factors are altitude, aspect, exposure and winter snow-covering, and they often become much more important in their effect upon the vegetation in other Arctic regions farther north—not only because of their still greater intensity but also, particularly in the case of snow-covering, because they affect much larger areas.

The four factors now under consideration are to a large degree interrelated. Thus as we go up a mountain (altitude) the situation tends to get windier and





Phot. 10. Reduced vegetation on detrital material of exposed hilltop. *Dryas octopetala* in flower, bottom left-hand corner.



Phot. 12. Psammosere on coast. *Elymus* (in foreground) binding weakly; real stabilisation here is effected by



Phot. 9. Open pine forest (*Pinus silvestris* f. *lapponica*) on dry rocky slopes in sheltered valley. Birches sub-dominant.



Phot. 11. Upland scrub of *Betula nana* and white-leaved

cooler (exposure<sup>1</sup>) and the *snow* in general to lie later and later, especially on north-facing slopes (aspect). To show the effect which each of these factors can have, more or less alone, they will now be considered briefly one by one.

Firstly *altitude*, acting of course through exposure, has as its most important effect the prevention of colonisation of upland regions by birch trees and other lowland dominants. Above the birch limit altitudinal climaxes of scrub and dwarf heaths are maintained, just as we see them north of the northernmost limit of trees, which lies about 100 km. south of North Cape. Higher on the mountains the vegetation, with the increased effect of exposure and reduction of the growing season by late-lying snow, becomes still further reduced. As we go farther and farther north the successive altitudinal zones of vegetation get lower and lower until at high latitudes the most extremely reduced Alpine types of community are found regularly at sea level. Norwegian Lapland is of fairly high latitude but has its climate tempered by the proximity of the Gulf Stream: deflected by the coast of Europe farther south this moves northwards up the west coast of Scandinavia and continues on towards Spitsbergen, with a smaller branch turning around North Cape and ending in Barents Sea. The result is that the sea around Norwegian Lapland does not freeze in winter, and while in exposed situations near sea level the vegetation may approach the true arctic-alpine type, especially on the north coast, it is more often subarctic in nature, and in the most sheltered situations may be quite luxuriant.

Nevertheless the effect of an increase in altitude is very marked, and is best illustrated by a series of photographs showing the changes which take place in the vegetation as we come out of a sheltered valley and climb to the top of an adjacent hill. The whole range in altitude from valley bottom to hill top may be no more than 600 or 800 ft., but the changes in the vegetation, resulting in the main from the increased exposure, are little less extreme than those which in the temperate regions would involve a rise of 6000 or 8000 ft.

Pl. XVIII, phot. 14 was not taken in a tropical forest with lianes and tree-ferns, although the shading and other effects make it resemble such a scene; instead it is an alder thicket with 5-foot ( $1\frac{1}{2}$  m.) high *Matteuccia Struthiopteris*, at the bottom of the sheltered Reisen Valley near the head of a fjord at a latitude of nearly 70° N. ! This is more than 200 miles within the Arctic Circle, and, with the possible exception of a few spots in one other valley about 60 miles away, must be about the most luxuriant vegetation so far north in the world.

Pl. XVII, phot. 9 shows the pine forest, with subdominant *Betula odorata*, developed on dry slopes above. The pines may be quite large trees.

<sup>1</sup> According to **Warming** (1909) the mean temperature of the warmest month of the year falls 0.6° C. for every 100 ft. rise in altitude.



Pl. XV, phot. 4, taken in winter when everything was snowbound, depicts the birch forest higher up, with the open pine forest visible in the valley below.

Pl. XVIII, phot. 13 shows a typical scene near the tree limit on gently undulating slopes. In the foreground outside the forest is an area showing rapid alternations of micro-physiographic conditions as well as of water and other edaphic factors—rocks, bogs and dry humps leading to polyclimax vegetation belonging to the upland scrub zone.

Pl. XVII, phot. 11 shows the zone of upland scrub which is typically developed above the limit of tree birches. It is a thick tangle limited to about 2 ft. in height by the depth of the snow-covering in winter, and consists of dark *Betula nana* mixed with conspicuous hairy, white-leaved *Salices* such as *Salix lapponum*, *glauca* and *lanata* with the usual complicated set of hybrids.

At higher altitudes *Betula nana* persists for the most part alone, but varies greatly in habit and luxuriance according to local conditions of exposure. Leach and Polunin (1932, Pl. XXVI, phot. 4), show tall scrub in the depression in the foreground, getting shorter and shorter with increased exposure and limiting of the winter snow-covering, until on the top of the ridge (left background) it is reduced to creeping axes pressed close against the ground (cf. Pl. XXVII, phot. 7 of the same paper).

Above the upland scrub lies a region dominated by *Empetrum* and *Vaccinia*, or in exposed places by *Dryas octopetala* or other high-arctic dwarf shrubs which are generally absent from the sheltered valleys.

Pl. XVII, phot. 10 shows the still greater reduction of the vegetation on the detrital soil of an exposed hilltop. The area corresponds with *fjældmark*, for there is a great deal of bare frost-shattered rock, and sparse open vegetation consisting largely of cryptogams of poor growth. A patch of *Dryas* is, however, to be seen in flower (bottom left-hand corner), and there was quite a lot of *Cassiope tetragona*.<sup>1</sup>

Finally Pl. XVIII, phot. 15, shows a scene where the snow drifts and lies very late on the higher mountains. Exposed rocks may have their lichens, and raised or particularly warm and sheltered areas (where the snow melts relatively early in the summer and allows woody plants to grow and sometimes to flower and fruit) may support a few dwarf heaths; but for the most part we get stony or muddy areas that may be almost or quite barren, and above, or even around them in places, perpetual ice and snow. This is almost exactly the situation over most of the area, even at sea level, of far northern regions such as Spitsbergen and Ellesmere Land.

Next the effect of *snow-covering* will be considered briefly. In the first place, as has already been said, it is important over considerable areas of

<sup>1</sup> Many Scandinavian botanists now recognise three Alpine vegetational zones, of which the middle one is characterised by the presence of *Cassiope tetragona*, but not of the other Ericaceous ground-shrubs or of *Empetrum*, which all remain in the lowest zone. The vegetation of the "upper Alpine zone" consists for the most part of cryptogams. In Norwegian Lapland such delimitation does not seem to be practicable, owing to the frequent telescoping.





Phot. 13. Mixed communities near tree limit. Fringe of open forest in background; in foreground upland scrub of *Betula nana* and *Salix* spp., alternating with mossy hummocks and areas of *Eriophorum* and *Carex* bog.



Phot. 14. Luxuriant thicket, dominated by *Alnus incana*, in sheltered valley. The ferns (*Matteuccia*) below are nearly the height of a man.



Phot. 15. Mountain summit with perennial snow patches. Closed dwarf vegetation in foreground becomes much poorer near the snow.

## POLUNIN—PLANT SUCCESSION IN NORWEGIAN LAPLAND

upland and other exposed regions in limiting the growth of tree and shrub types which here cannot grow above the usual winter level of the snow. Secondly it is important in forming patches on mountains or in hollows where it drifts deeply every year. The growing season in the centre of the patch may be reduced by the lateness of its melting to 3 or 4 weeks or even less, so that the community is maintained at or near a pioneer moss or algal stage, with a ringed zonation of subclimaxes dominated by higher and higher life forms where the influence of the snow becomes less and less.<sup>1</sup> Such late snow patches occur not far above (and sometimes within) the birch forest in Lapland, and farther north become more and more important, until at very high latitudes the situation is reversed and we have land covered with permanent or at least perennial snow and ice, except for occasional raised areas that are bared for a brief period in summer, and become populated by plants that can vegetate quickly. This is illustrated in Pl. XVIII, phot. 15 which has in the foreground almost continuous dwarf vegetation, but nearer the edge of the snow (as it is in late summer) the ground is largely barren.

Thirdly there is the effect of *aspect*, which as we journey farther north becomes more and more limiting to the vegetation with the very late melting or non-melting of snow on north-facing slopes. Remarkably enough, in Lapland and Labrador the effect of aspect is still, as in the Mediterranean, chiefly manifest at low altitudes of the more continental regions in the drying out of south-facing slopes by the sun, so that those facing north are more luxuriantly vegetated. On such slopes there are herbs, ferns and mosses instead of lichens and xeric undershrubs (Leach and Polunin, 1932). On the other hand, with an abundant supply of ground water—so long as this is not stagnant—the most luxuriant vegetation of all is developed upon (or at the bottom of) the sunny south-facing slopes in the most sheltered valleys.

Lastly *exposure* may be of primary importance in determining the vegetation locally, as became abundantly clear in considering the effect of altitude. For exposure to winds is at least one of the main factors determining the limit of trees both in altitude and in latitude, although this is partly bound up with the question of snow-covering. In winter the snow provides a comparatively warm protecting blanket, damping down the fluctuations of air temperature; but such areas as are blown clear of snow have not only as a rule no real trees, but also, even in Lapland, are largely shorn of other forms of vegetation by desiccating winds and hard-blown snow. The same areas—particularly near the coast and on mountains—that are exposed in winter are generally windy in summer, and in the face of these winds even the few plants that can exist will exhibit very little growth. Most typically they remain as closed tussocks or rosettes—forms which may guard them against excessive transpiration but can have little effect against low temperatures, which have to be withstood by internal means.

<sup>1</sup> Cf. Polunin, 1934.

Then at very high latitudes, in Spitsbergen, Ellesmere Land and the coastal regions of Siberia and Arctic America, the air is cool even in summer, but with the high insolation of a long-lasting "midnight sun" the plants may be well warmed by radiation to a temperature favourable for quite rapid growth—that is, where there is shelter from the almost perpetual winds bringing cold air in contact with them. In this wind, even more than out of the sun, all is cold—not only does the wind increase transpiration and thereby lower turgor and temperature, but its everlasting impingement prevents proper heating from solar radiation, and the writer knows considerable areas of Spitsbergen at a latitude of nearly 80° north that are better vegetated (largely because they are sheltered) than almost the whole of the very windy island of Akpatok in Hudson Strait more than a thousand miles farther south.

#### SUMMARY

Though of arctic position and severe winter climate, the more continental parts of the extreme north of Scandinavia have a summer which is warm and relatively favourable to plant growth, the sun being visible throughout the 24 hours and frosts usually absent for several weeks on end during June and July. There are described the three main *seres* or successions of plant communities that in each case start with the invasion of bare areas and in time lead up to the climatic climax vegetation of the region. This climax is an open birch forest of scattered, scrubby trees with a ground layer of dark green undershrubs which in dry areas are frequently interrupted by patches of light grey lichens. The main *seres* are quite comparable with those of temperate regions:

(i) The succession of plants invading lakes leads to the raising of the floor and in time the disappearance of the open water as more and more vegetable material is deposited; this *hydrosere* comprises a series of eight more or less well-marked stages, starting with a submerged aquatic stage and continuing progressively through the floating leaf, reed swamp, moss colonisation and various shrub and tree stages to the climax.

(ii) In the *psammosere* on dry sands five stages are recognised, with sand-binding grasses, mosses or undershrubs as the pioneers.

(iii) The *lithosere* or succession on dry exposed rock surfaces is generally very slow. It has a maximum of eight stages of which the first two or three, as in the other *seres*, are non-essential and termed *proseral*. In the lithosere the great importance of crevice communities is recognised. The *mesosere* or succession on the damp "soil" which is frequently seen in the Arctic in summer, is described, and also the pine forest post-climax which is developed in the more sheltered valleys; finally the effect of man and pasturing animals, especially reindeer, on the vegetation.

Throughout all the *seres* there can be seen the principle of convergence of water relations, the wet habitats becoming drier and the dry habitats wetter,

as the climax (of intermediate soil-water content) is approached. But the normal course of succession may be variously modified through the influence of differences in altitude, aspect and exposure, and of the persistence of the snow-covering, which may yield conditions inimical to the growth of trees, and in some places even of shrubs. These influences become of much more general importance farther north in Spitsbergen and other high-arctic lands where the snow melts still later or not at all; but even in Lapland they may cause the successions to be terminated locally at an early dwarfed stage dominated in some cases by quite primitive plants—at least where higher types are excluded by their inability to complete their life processes in the greatly shortened growing season.

## REFERENCES

- Cooper, William S.** "Seventeen years of successional change upon Isle Royale, Lake Superior." *Ecology*, **9**, 1928.
- Du Rietz, G. E.** "Några iakttagelser över myrar i Torne Lappmark." *Bot. Notiser*, 1921 and several other papers.
- Fries, Thore C. E.** *Botanische Untersuchungen im nördlichsten Schweden*. Uppsala and Stockholm, 1913.
- Godwin, H. and Tansley, A. G.** "The vegetation of Wicken Fen." *The Natural History of Wicken Fen*, Part v. Cambridge, 1929.
- Leach, William.** "On the importance of some mosses as pioneers on unstable soils." *This JOURNAL*, **19**, 1931.
- Leach, William and Polunin, Nicholas.** "Observations on the vegetation of Finmark." *This JOURNAL*, **20**, 1932.
- Nordhagen, Rolf.** *Die Vegetation und Flora des Sylenengebietes*, Oslo, 1928. (Skrifter utgitt av det Norske Videnskaps-Akademi i Oslo, 1927).
- Norman, J. M.** *Norges Arktiske Flora*. Kristiania, 1894.
- Polunin, Nicholas.** *Russian Waters*. London, 1931.
- Polunin, Nicholas.** "The vegetation of Akpatok Island. Part I." *This JOURNAL*, **22**, 1934.
- Warming, E.** *Ecology of Plants*. Oxford, 1909.

# MARINE ALGAL ECOLOGY AND THE EXPOSURE FACTOR AT PEVERIL POINT, DORSET

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(*With Plate XIX and seven Figures in the Text*)

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## INTRODUCTION

THIS investigation was undertaken in the conviction that at the present time real advance in the comprehension of marine algal ecology and the factors determining distribution can best be obtained by detailed studies of small well-defined areas. A considerable amount of scattered information is available as to the species of marine algae to be found around the coasts of the British Isles, but there are few exact data defining the ecological position of these species or their relation to the tidal flow, and consequently it is difficult to correlate one region with another.

Peveril Point was chosen for this investigation because of the accessibility of the rocks, the distinct zonation visible, and the peculiarities of the geological formation, which enable the effect of vertical and inclined surfaces and of northern and southern aspects to be observed.

## THE AREA SURVEYED

The two reefs of rock at Peveril Point which form the main subject of these observations are on the south coast of England, lat. 50° 35' N. and long. 1° 55' W., and constitute the northern boundary of Durlston Bay,

Swanage (Fig. 1), the more northerly of the two (known here as Reef I) dividing Durlston Bay from Swanage Bay. At Mean Low Water Ordinary Tides this reef is exposed for a length of about 230 ft. running almost due east from the shore (Fig. 2). The second reef (known here as Reef II) lies approximately 216 ft. to the south and is exposed for a distance of 340 ft. at M.L.W.O.T.

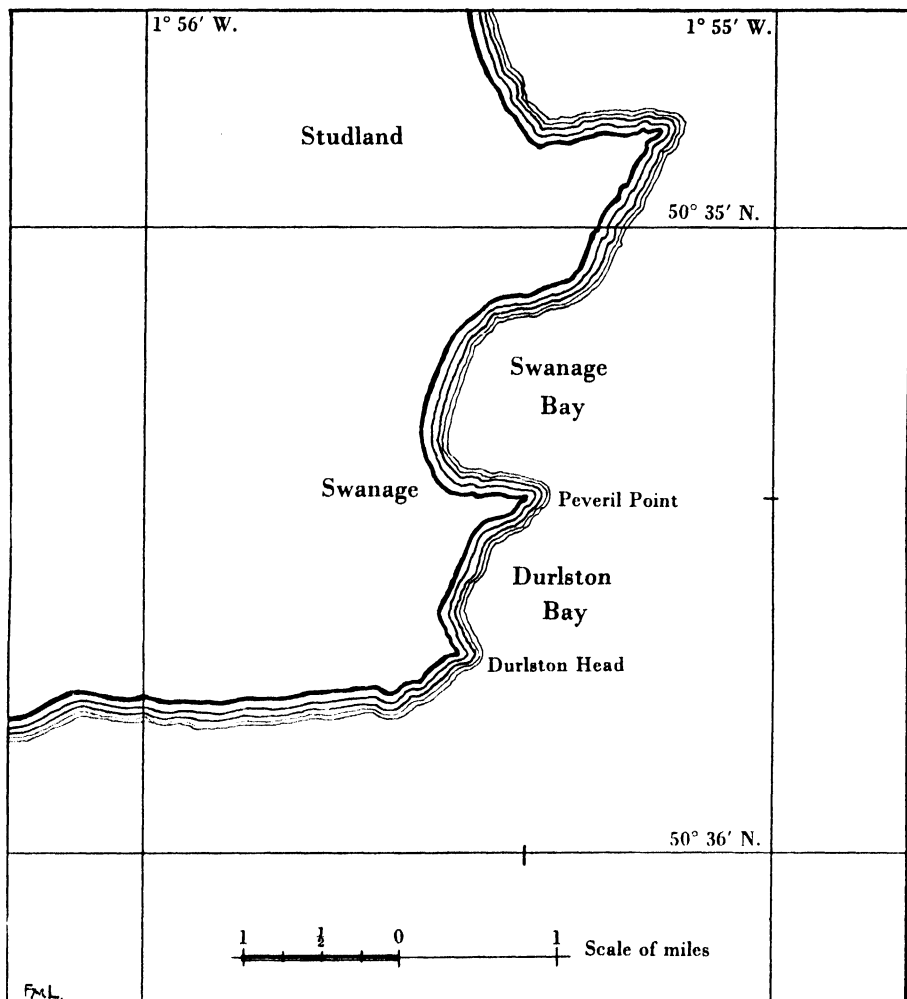


FIG. 1. Map of the Swanage area, showing the position of Peveril Point.

At their highest points Reefs I and II rise 7·6 and 8·5 ft. respectively above M.L.W.

These two reefs form an interesting contrast, for though formed from the same strata, their main slopes lie in opposite directions (Pl. XIX, photos. 1 and 2). The northern face of Reef I is, for the most part, a vertical wall. The southern face along the whole length of that reef slopes gradually to the



sea floor at an angle of 70–75°. In Reef II the reverse is the case. The northern face is sloping, the angle of slope being 70° from the vertical, giving in the highest parts of the reef a width of some 30 ft. of rock face above L.W.M. On the southern face of this reef the vertical drop is only broken here and there by occasional jutting-out shelves of rock.

The cliffs and shore at Peveril Point are formed of rocks of Upper Purbeck age and show in a marked degree minor folding, both anticlinal and synclinal. In consequence of the latter, the beds composing these two main reefs dip towards each other and represent the same geological horizon, the Broken Shell limestone or "Burr". This limestone is very hard and is crowded with fossilised remains of *Unio*, *Limnaea*, *Viviparus* and fish. The shore and fore-shore forming the "basin" between the two reefs is composed almost entirely of limestone fragments varying in size from large boulders to small pebbles (Pl. XIX, phot. 1).

#### METHODS OF SURVEY

A complete triangulation survey of the coast line at Peveril Point, together with the two reefs under observation, was made for me by Mr Frank Laing, F.I.A.S., and I am most grateful to him for the endless trouble which he took and also for his help in the calculation of the tides and in making the diagrams. The survey was checked up with the Dorset Sheet LVII of the 1/2500 Ordnance Survey. A number of positions (here called lines) were chosen on the two reefs, five on Reef I and nine on Reef II, and their levels were corrected to the nearest hundredth of a foot. All levels were reduced from a bench mark (32.20 ft. above Ordnance Datum) situated on a large stone on the top of the cliff below the coastguard's look-out, and the readings on the traverses and cross-sections were checked back to this bench mark. The true bearings and the distance of each line from the next are shown in Table I, and a general "lay-out" plan

Table I

*True bearings through centre longitudinal line and distances  
of traverses on northern reef (Reef I)*

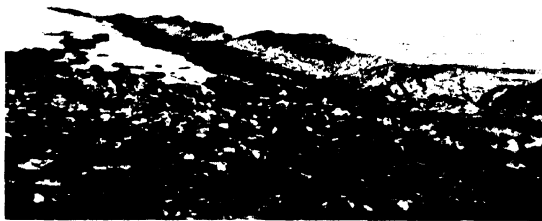
Line	Distance	Bearings
1 to 2	33' 0"	260°
2 to 3	49' 0"	257°
3 to 4	49' 0"	259°
4 to 5	29' 0"	261°

*True bearings through centre longitudinal line and distances  
of traverses on southern reef (Reef II)*

Line	Distance	Bearings
1 to 2	30' 0"	273°
2 to 3	44' 0"	276°
3 to 4	32' 0"	280°
4 to 5	12' 6"	272°
5 to 6	29' 0"	269°
6 to 7	51' 0"	269°
7 to 8	19' 6"	265°
8 to 9	21' 9"	262°
9 to X	Check reading	251°



Phot. 1. Sloping southern face of Reef I. Foreshore covered with low boulders.



Phot. 2. Northern face of Reef II with the bare zone dividing the upper from the lower associations.



Phot. 3. End of Reef II at M.L.W.S., showing *Laurencia-Corallina* association with *Himanthalia* and *Laminaria* below.



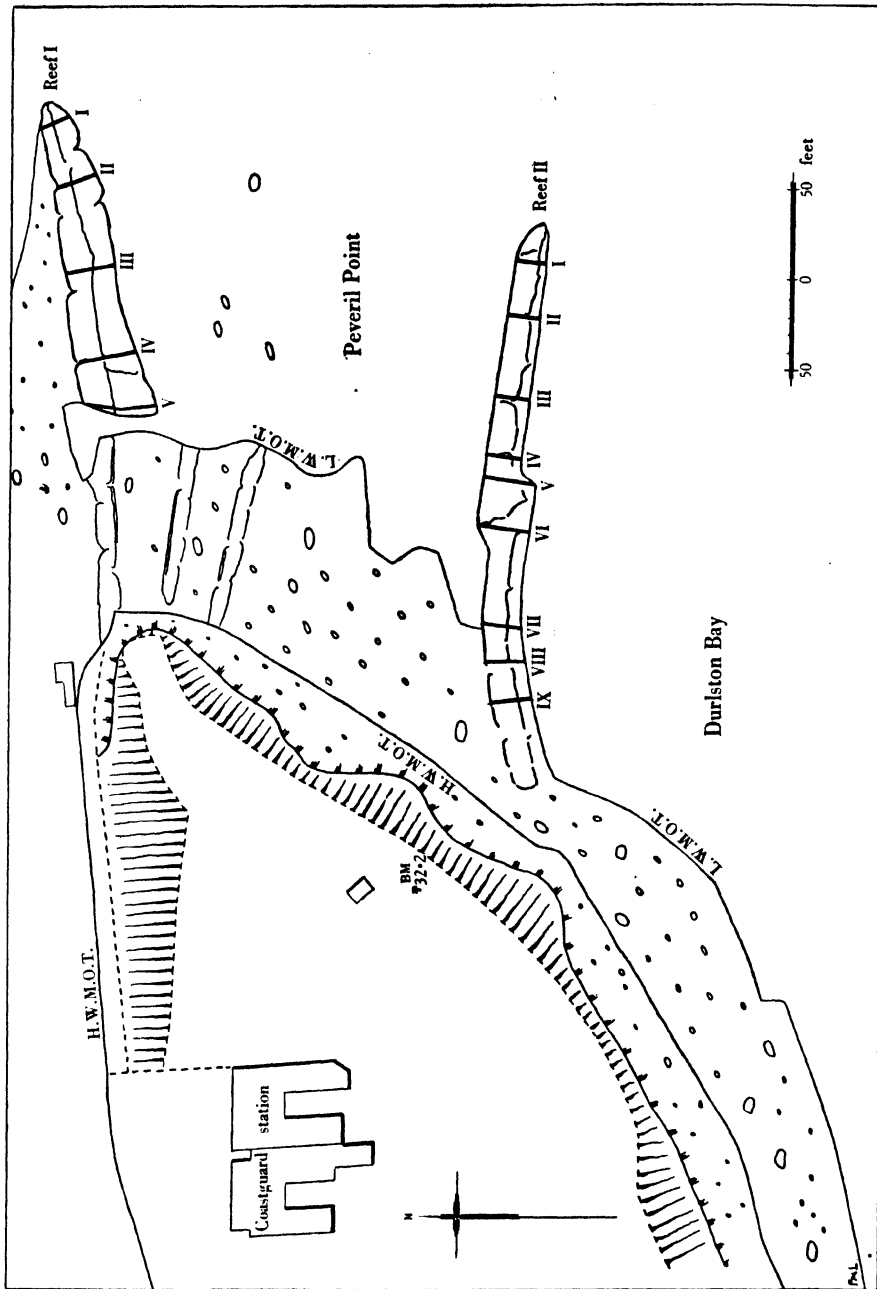


FIG. 2. Map of Peveril Point, showing Reefs I and II and the position of the surveyed lines (numbered).

enlarged from the Dorset Sheet LVII of the 1/2500 Ordnance Survey, and showing the lines selected for special observation, is given in Fig. 2.

The reefs were visited at intervals of two to three months throughout a year, the dates of the visits being as follows: April 7th–17th, 1934. June 8th–11th, 1934. September 7th–10th, 1934. December 8th–9th, 1934. April 1st–4th, 1935. On each of these visits careful observations were made of the tidal data and the littoral vegetation. No attempt was made at an exhaustive search for every kind of alga to be found on the reefs, but certain definite species were selected, more especially those that were present in such large quantities as to dominate the vegetation. At each of the five lines on Reef I and the nine on Reef II, the upward and downward limits of these algae or algal associations were measured, recorded, and later plotted on a chart. The eastward and westward limits along the reefs were noted and collections were made of the principal species in each association. In this way it was possible to obtain a complete picture of the occurrence of each selected association upon the given area of the shore and also to trace its survival or disappearance during the course of the year.

“Chart Datum” was selected as the standard datum line and the measurements of the reef and the algal associations are given as vertical heights above this line. Chart Datum (C.D.), the zero to which the heights of the tide are referred in the *Admiralty Tide Tables*, is defined as “a plane so low that the tide will but seldom fall below it” and with a few exceptions this approximates to the level of Mean Low Water Springs. It was selected by Johnson and York (1915) as the Datum Line for their measurements at Cold Spring Harbour, and is the level implied, if not always defined, as the lower limit of a “littoral” or “lower littoral” zone by many other writers. For these reasons it was thought better to refer all measurements to this datum line rather than to “Ordnance Datum”, the Land Survey Datum throughout the British Isles. Coleman (1933) at Wembury Bay gives the measurements as vertical heights above O.D., on the ground that this level is constant throughout Great Britain, but measurements referred to this level do not give any indication of the position of a plant or animal with reference to the tidal phenomena. In any case measurements can easily be converted from one to the other, for O.D. is 8.42 ft. above C.D. at Devonport (Wembury) and 2.7 ft. above C.D. at Peveril Point.

#### THE EXPOSURE FACTOR

Although the primary aim of this investigation was the attempt to obtain precise data as to the range of certain marine littoral associations, it was obvious that these would be of far greater value if correlated with the factors that are known to limit these associations, such as the intensity of light, temperature, the nature of the substratum, and exposure. While realising that these factors naturally interact, the exposure factor was selected for special

study since it seems to be of cardinal importance, and variations of light and temperature are closely related to the duration of the periods of emergence and submergence. By a study of the diurnal rise and fall of the tide at Peveril Point over longer and shorter periods an attempt has been made to estimate the range of exposure which is tolerated by each association, and the effect of the exposure factor in the limitation of the growth of the associations.

#### TIDAL PHENOMENA AT PEVERIL POINT

Entirely accurate tidal data for Peveril Point do not exist. In a letter from the Hydrographic Department of the Admiralty, Captain Edgell, Hydrographer, says: "No information for exact times or heights of low water (at Peveril Point) is available in this Department."

The nearest place for which these data are published in the *Admiralty Tide Tables*, Part I, is Portland, a distance of some 35 miles along the coast. But although this is nearer in mileage than Southampton, the latter was found to be the more suitable port of reference, and is regarded as such in the official *Tide Tables*, owing to the double high water which occurs there, as at Swanage. Calculations of high water at the secondary port of Swanage were made on Southampton from the data given in the *Tide Tables*, Part I; 2 hours 33 min. before the time of high water at Southampton represents the time when the tidal wave, moving up the channel from the west, would reach Swanage.

The times of high water obtained in this way were frequently checked at Peveril Point on calm days by observations of the rise and fall of the water at measured points on the reefs, and were found to be substantially correct. The discrepancy did not appear to be more than 10 min. in either direction.

Low water "should be approximately  $7\frac{1}{4}$  hours after the time of the first high water at Swanage" (Hydrographic Department of the Admiralty). According to the local authorities at Swanage the time of low water varies between 6 and  $7\frac{1}{4}$  hours after high water, depending largely on the direction of the winds. In practice, on a calm day low water was found to agree with the Admiralty estimates, and in the following graphs the effect of the winds has of necessity been disregarded.

The phenomenon of a double tide, which is found along the coast from Portland Bill to Southampton, occurs here. In the eastern part of the tidal area (Southampton, Portsmouth and the Solent), there is a double high tide with an interval of 2 hours or less between the two high waters. Passing westward the interval increases, and is approximately  $2\frac{1}{2}$  hours at Peveril Point. Still further west, e.g. at Portland, the second rise of the tide is so long after high water that it approaches the following low water and two low tides (the "Gulder") are experienced here.

At Peveril Point then, the course of the tides is as follows (see Fig. 3). The first high water ebbs for at least  $2\frac{1}{2}$  hours, the length of this time depending largely on the strength of the prevailing wind. When it is blowing on shore

(i.e. east, north-east or south-east) there is very little fall to second high water and the tide remains penned up for 3 hours or so before the ebb commences. On a calm day the water will fall 2 ft. or even more in the first 3 hours. During the next hour a rise will occur of 1-2 ft.; if the wind is blowing on shore, the water will be forced up to an even higher level than that of the first high water; if the wind is blowing off shore (west, north-west, or south-west) this rise does not occur, and the water remains at the same level for an hour or more. The ebb then again takes place, slowly at first and during the last hour and a half more rapidly, until, about  $7\frac{1}{4}$  hours after first high water, low water is reached. The water remains stationary at this level for about half an hour, and then rises, at first rapidly and later more slowly, to high water again. This rise occupies some  $4\frac{1}{2}$  hours. The whole course of the tides at Swanage is, however, greatly affected by the direction and strength of the prevailing winds.

At spring tide, the range of the tides, that is "the difference in level between any high water and the following low water" is between 6 and  $6\frac{1}{2}$  ft., and at neaps it varies considerably, ranging from 4 ft. 6 in. to only a few inches. The mean height of the tide at springs is 6.2 ft. and at neaps 4.2 ft.

The more important tidal levels for Peveril Point are set out in Table II. Calculations of the height of high water were made in accordance with the figures given in the *Admiralty Tide Tables*, Part II, for the secondary port of Swanage, i.e. 7.0 ft., are subtracted from the published figures for Southampton for springs, or 7.2 ft. for neaps. The data obtained were checked from time to time on the measured reefs at Peveril Point and were found to be substantially correct. Extreme high water springs occurred on January 19th and again on July 29th. The height of low water at Peveril Point (springs or neaps) corresponds with that given for Portland in the official *Tide Tables*. Extreme low water springs was on February 15th.

Table II. *Tidal levels at Peveril Point*

	Vertical height (ft.) above C.D.
Extreme High-Water Springs (E.H.W.S.)	8.0
Mean High-Water Springs (M.H.W.S.)	6.2
Mean High-Water Neaps (M.H.W.N.)	4.2
Mean Sea-Level (M.S.L.)	3.0
Extreme (lowest) High-Water Neaps (E.H.W.N.)	2.6
Extreme (highest) Low-Water Neaps (E.L.W.N.)	4.0
Mean Low-Water Neaps (M.L.W.N.)	2.8
Mean Low-Water Springs (M.L.W.S.)	0.7
Chart Datum (C.D.)	0.0
Extreme Low-Water Springs (E.L.W.S.)	- 1.2

From these tidal data it has been possible to calculate the periods of emergence and submergence undergone at different levels on the shore over shorter or longer times, and then to relate these to the algal associations at these levels.

*(a) Exposure on a single day (April 14th, 1934)*

The tides on April 14th were spring tides but by no means the highest springs of the year; the range of the morning tide was only 5·4 ft. and of the afternoon 6·1 ft. The day was very calm and the rise and fall of the tide was observed and timed throughout the hours of daylight. The position on the reef reached by the water at first and second high water was noted and marked on a measured chart giving the vertical levels on the reef, and thus the vertical height of the tide above C.D. could be ascertained. This was found to agree with the height of the tide as calculated on Southampton. In the same way low water was noted and was found to agree with data obtained from Portland. The tidal curves for two high waters on April 14th were drawn to scale (Fig. 3) and from these can be calculated the hours of exposure at different levels on the shore during each of the tidal periods. The first tidal period (a) extends from second high water at 22 hrs. 16' on April 13th to second high water at 11 hrs. 10' on April 14th (12·9 hours), the second period (b) from 11 hrs. 10' on April 14th to 23 hrs. 35' on the same day (12·4 hours). The number of hours' continuous exposure at each level and the percentage exposure are set out in Table III.

Table III. *Number of hours' exposure and percentage exposure at different levels on the shore on April 14th, 1934*

Vertical height on shore (ft.) ...		8	7	6	5	4	3	2	1	C.D.
(a) No. of hours' exposure		12·9	12·9	12·0	9·3	6·1	4·7	3·2	1·4	0
% exposure		100·0	100·0	92·8	72·1	47·2	36·4	24·8	10·8	0
(b) No. of hours' exposure		12·4	12·4	10·9	8·6	6·2	5·0	3·5	2·0	0
% exposure		100·0	100·0	90·6	69·3	50·0	40·3	28·2	16·1	0

*(b) Average exposure of four fortnights*

To select one curve such as this and calculate exposures from it gives, of course, no accurate picture of the conditions to which the algae at various levels are subjected, since the range of the tide varies so greatly from springs to neaps. In an endeavour to obtain a more complete view of the exposure factor four similar curves were therefore drawn over periods of 14 days. Four such fortnights were selected in the four quarters of 1934, i.e. spring equinox (March 12th–25th), midsummer (June 18th–July 1st), autumn equinox (September 19th–October 2nd), and midwinter (December 16th–29th). From these curves the number of hours of exposure at different levels was estimated in the manner described and the average exposure over a fortnight could then be calculated (see Table IV, column I).

The range of the tide in midwinter is smaller than at the other three selected periods and this finds its corollary in the fact shown in column I that in midwinter the exposure is greater in the upper reaches of the littoral region



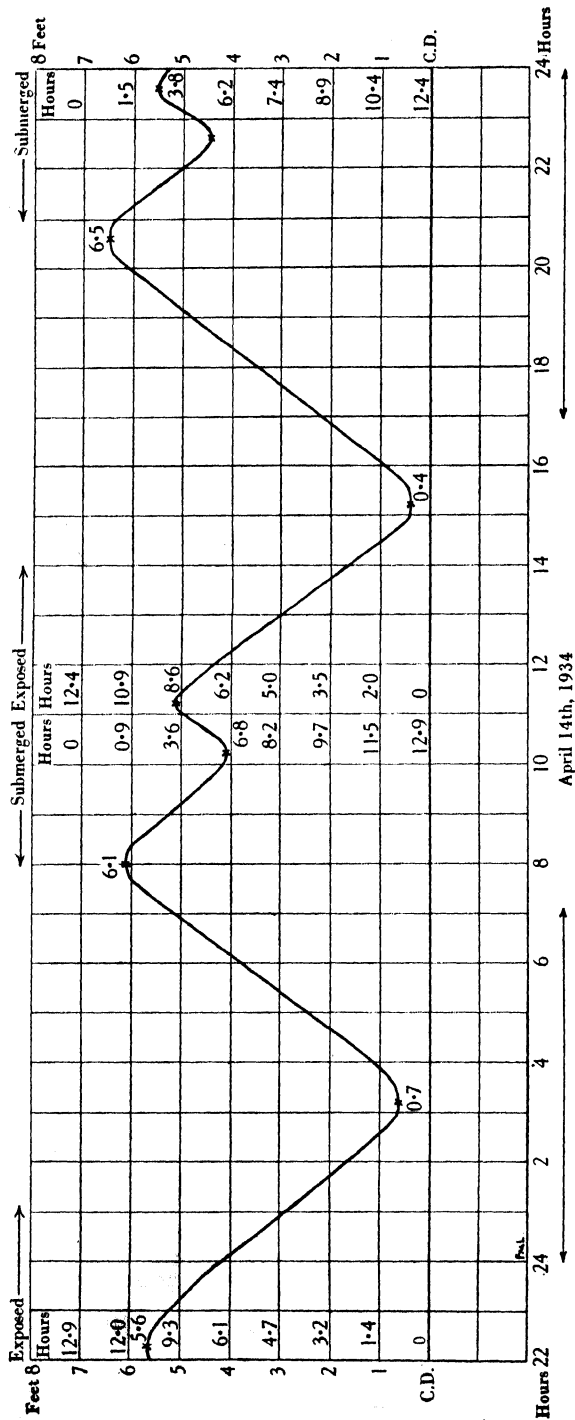


Fig. 3. Tidal curve for two successive tides from 22 hours 16 min. on April 13th to 23 hours 35 min. on April 14th. The second high water is shown occurring from 2 to 2½ hours after the first. The number of hours of emergence and submergence at different levels are shown in the columns at left and right of each tidal curve respectively.

than at other times of the year and is also less towards mean low water. Another interesting fact brought out by column I is that though in the upper levels of the tidal range (8 to 6 ft. above c.d.) there is comparatively little variation in the period of exposure in these four fortnights and similarly in the lower levels (+2 ft. to c.d.), yet in the middle region (3 to 5 ft. above c.d.) there is considerable variation. This is seen more clearly in column II of the same table, where the percentage periods of emergence in these four fortnights are compared. These exposure figures have been plotted in Fig. 4 in the form of four curves, and this shows that the widest variation in the amount of exposure undergone at the various levels lies between 2.5 and 5 ft. above c.d. and may amount to as much as a difference of 23 per cent. of the exposure period (at 4 ft. above c.d.). The variation in the exposure at the four selected periods is set out in Table IV, column III, and it will be shown later that this variability in the middle littoral region has considerable bearing upon the distribution of algal forms in that region.

Table IV. *Number of hours and percentage period of exposure per day calculated over a fortnight (columns I and II) and over four fortnights (column IV). Column III shows the maximum variations in the periods of exposure (expressed as percentages) which occur in the four fortnights*

	Height in ft.	I. Average no. of hours' exposure per day (24 hours)				II. Period of exposure expressed as a percentage (see Fig. 4)				III. Maximum variation in periods of exposure (%) in the four fortnights (see Fig. 4)	IV. Exposure in the four fortnights		
		Spring equinox (Mar. 12th-25th)	Midsummer (June 18th-July 1st)	Autumn equinox (Sept. 19th-Oct. 2nd)	Midwinter (Dec. 16th-29th)	Spring equinox	Midsummer	Autumn equinox	Midwinter		Total no. of hours exposure	Average no. of hours ex- posure per 24 hours	Percentage exposure (see Fig. 6)
7.8 = extreme H.W.S.	8	24	24	24	24	100	100	100	100	0	1344	24	100
	7	23.7	23.8	23.3	24	98.8	99	97.1	100	3.9	1328	23.7	98.8
6.2 = M.H.W.S.	6	22.2	22.7	21.3	24	92.5	94.6	88.7	100	11.3	1274	22.6	94.5
	5	19.2	20.5	18.4	22.2	80	85.4	76.6	92.5	15.9	1124	20.1	83.8
4.2 = M.H.W.N.	4	15.8	18.7	13.2	16.8	65.7	78	55	70	23	903	16.1	67.1
	3	7.2	9.5	4.5	8.4	30	39.6	18.8	35	20.8	415	7.4	30.8
2.8 = M.L.W.N.	2	3.0	2.8	1.9	1.8	12.5	11.7	7.9	7.5	5.0	134	2.4	10.0
0.7 = M.L.W.S.	1	1.3	1.2	0.7	0	5.4	5.0	2.9	0	5.4	45	0.8	3.3
	c.d.	0.25	0.2	0.09	0	1.0	0.8	0.04	0	1.0	9	0.14	0.6

(c) *Average exposure over a year*

In order to obtain a more complete picture of the exposure at different levels, the hours of exposure calculated from the four fortnights were added together, averaged and percentaged (Table IV, column IV) and this result is given in the form of a curve (Fig. 6, p. 415) showing the average amount of exposure undergone at different vertical levels on the shore.

(d) *The splash zone*

These figures relating to the periods of emergence are calculated on the assumption that the flow of the tide has not been interfered with by winds. This is rarely the case, and since the prevailing winds at Peveril Point are on-shore and the reefs are to some extent sheltered by the cliffs from the off-shore winds it may be assumed that on the whole the water will stand

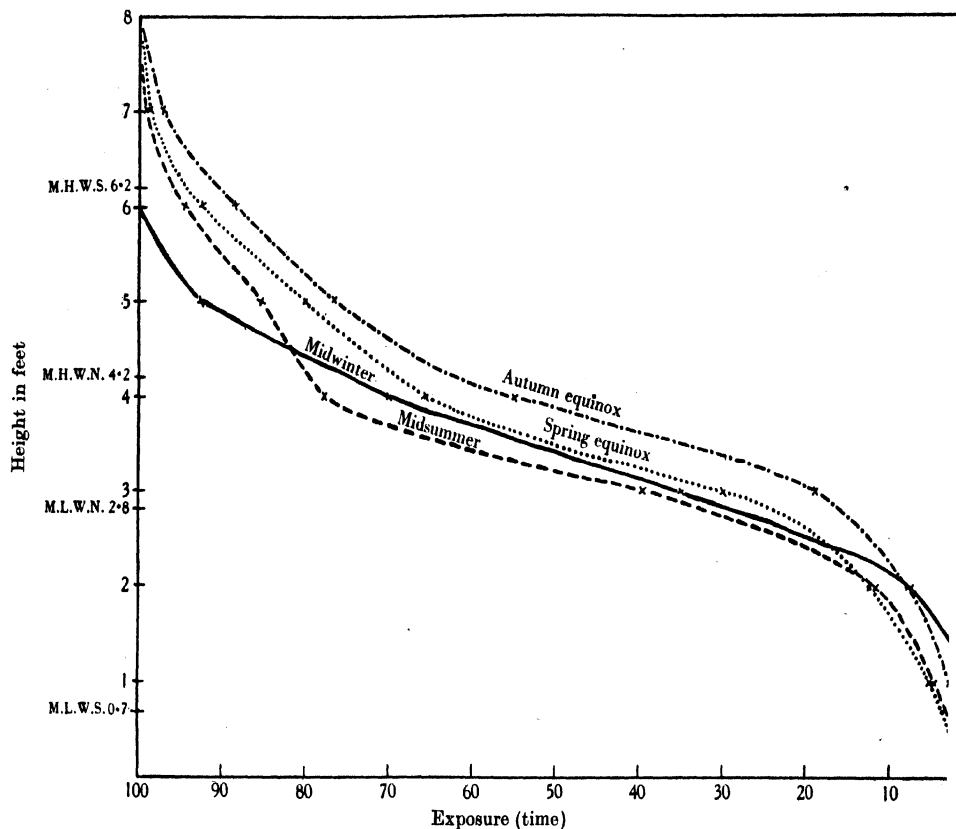


FIG. 4. Curves showing the average period of exposure (expressed as a percentage) at different heights on the shore for the four fortnights of spring equinox, midsummer, autumn equinox, and midwinter.

higher and the exposure be less than that shown by the chart. It is always difficult to estimate the extent of this rise in the water when spread over a whole year, as in the summer there are frequently calm days with little or no wind or spray, while in winter the wind and spray are sometimes so strong that even at midtide it has been difficult to set foot upon the highest part of the reefs. According to the local coastguards the autumn and winter of 1934 were unusually mild and calm, and though Coleman (1933) has assumed at Wembury Bay a 2-ft. splash zone, as Johnson and Skutch did at Mount Desert

Island (1928, I), possibly a 1-ft. splash zone would represent the average at Peveril Point during 1934. This splash zone has not been taken into consideration in reckoning the exposures or in the following notes, as it is such a variable quantity. It has, however, been allowed for in Fig. 6 (right-hand column) and its effects on the algal associations can be seen there. On the lower levels of the shore such a splash zone will do much to reduce the period of emergence to a minimum, but in the middle and upper levels the hours of emergence will still be long and the consequent desiccation considerable. Even on a rough day when there is much spray, in warm weather *Porphyra* dries out and sticks as a glistening sheet on the rocks as the tide falls, *Fucus spiralis* is hard and brittle, while the few algae on the upper levels of the shore are plastered to their limpet shells and boulders.

## THE ALGAL ASSOCIATIONS AND THE EXPOSURE FACTOR OF REEF II

### (a) Terminology

The use of terms in marine algal ecology has always been somewhat vague and no attempt is made here to go into this disputed question. The word "association" is used in this paper in the sense given to it by Cotton (1912), to mean those portions of the vegetation which obtain their characteristic stamp through one or more algae which predominate. A number of associations combine to form a formation and at Peveril Point we are dealing with a rocky shore formation. The word zone has recently come into some prominence and has been variously used in place of formation or association. But "zone" or "zonation" are better employed to denote the position of an association with reference to the tidal phenomena, for they imply some estimate of the relative period of emergence or submergence and it is in this sense that they are used here. Names for further subdivisions within the associations will undoubtedly be needed in the future, but at present our knowledge of transient species is so fragmentary that it would be premature to suggest fresh terminology.

### (b) The associations of Reef II

An account of the algal associations of Reef II is given first, since observations were made here over a greater area than on Reef I and a fairly complete view of the littoral vegetation was obtained. Reef II is connected with the coast by a stretch of low boulders. It consists of three main regions separated from one another by creeks. In the first part of the reef, that nearest the shore, the highest point is 8.48 ft. above C.D. and is above the level of high spring tide, but is frequently covered by the spray at high and midtide. The second and third parts of the reef are almost entirely submerged at high spring tide and parts are included in the spray zone at neap tide. Lines 8 and 9 lie in the first part of the reef, lines 7-5 in the second part and lines 4-1 in the third part (Fig. 5).

Standing on the shore and looking along Reef II at low water, long horizontal lines of colour can be seen running the length of the north or sloping face (Pl. XIX, phot. 2). These are the algal associations, each with some dominant species which gives colour and character to that area. The measurements and descriptions of these associations follow, as seen in April and modified throughout the year, while their distribution and the relation of one association to another are seen in Fig. 5. An attempt has been made to correlate the facts of distribution with those of exposure and to interpret the units of the associations in terms of emergence and submergence (see Fig. 6).

#### A. *Blue-green association.*

This is the highest association present. It occurs only on the north face of line 9, extending from the crest of the reef (+8.48 ft.) to +7.15 ft. The association is therefore above M.H.W.S. and is only washed occasionally in its lower reaches by extreme spring tides. On the south (vertical) face of the reef it grows down to +6.7 ft. at this point and then ceases abruptly. That it is only found in this one region is probably accounted for by the fact that no other part of the ridge rises above +7.15 ft. and this represents the lower limit of the growth of *Rivularia atra* and *Calothrix scopulorum*, the dominant algae of this association. The other macroscopic species are scattered and stunted plants of the linear form of *Porphyra umbilicalis* and *Enteromorpha intestinalis*, together with patches of *Lichina pygmaea*. This lichen is very variable in distribution, prefers the vertical south face to the sloping north face, and was absent in the summer months. In the autumn, numerous sporelings of *Fucus* spp. and *Enteromorpha intestinalis* were found among the blue-greens, growing principally in the looser patches of *Calothrix*. Apparently the *Fucus* sporelings never develop to any size, as macroscopic plants of *Fucus* do not grow at any period of the year at this height on the reef.

The blue-green association depends for moisture entirely on the spray and rain. It is a matter of frequent observation that the algae undergo severe desiccation and are frequently found clothing the rocks in dry, hard and cracked sheets.

*Rivularia atra* and *Calothrix scopulorum* are not often mentioned in literature on algal ecology, though Børgesen (1905) notes that the latter belongs to a formation which covers the rocks to "more than two feet above the level of the sea and down to the *Corallina* formation". Its upper limits are the same at Peveril Point, though it does not extend so low. Perhaps as a result of its limited and exposed position here, *Rivularia atra* does not survive the summer months as it does on the Faeroese coasts. The position of *Lichina pygmaea* is peculiar. At Clare Island it is always found "between the tide marks...it commences immediately below *Pelvetia* and extends downwards to within a few feet of low water" (Cotton, 1912). At Peveril Point it begins its growth in approximately the same position but scarcely extends down as





far as M.H.W.S. and then dies out. The second species which is found at Clare Island, *Lichina confinis*, grows well above high water mark there but does not occur at all at Peveril Point.

### B. *Porphyra association.*

Immediately below the dark blackish patch which represents the blue-green association, a purple glistening region can be seen in the winter and spring months consisting of *Porphyra umbilicalis* forma *linearis*. The *Porphyra* fronds are long, narrow and fertile, as shown by the white margin surrounding each thallus where the spores or spermatia have been shed. This association, exposed at mid- and low-water, forms a horizontal line the whole length of the reef, with the exception of the last 50 ft. where the crest of the rocks falls below the lowest limit at which this species will grow; the measurements which were made of the vertical distribution of the association are summarised in Table V (see Fig. 5).

Table V. *Distribution of Porphyra umbilicalis on Reef II, April 1934*

		Vertical height (ft.) above c.d.							
Line ...	1 and 2	3	4	5	6	7	8	9	
North face	—	+5.0 to +4.0	+5.5 to +4.5	+5.8 to +3.8	+7.0 to +4.6	+6.3 to +5.8	+6.7 to +4.9	+7.1 to +5.5	
South face	—	—	—	+5.8 to +4.7	+7.0 to +4.2	+6.3 to +5.4	—	—	

It will be seen that this species grows from 7.1 ft. above c.d. to a lower limit of 3.8 ft., and the rougher the situation, the broader the zone. The lower boundary is very sharply marked and few plants stray over it into the next region. From +7.1 to +6.0 ft. may be called a pure *Porphyra* stand. No other algae are found here with the exception of *Fucus spiralis*, and some *Scytosiphon lomentarius*, *Punctaria plantaginea*, *Enteromorpha compressa*, *Polysiphonia variegata* and *Ceramium rubrum* in creeks and small pools among the rocks. From +6.0 to +3.8 ft., *Fucus spiralis* becomes dominant in several places and *Porphyra* shelters beneath it. *Enteromorpha* and *Scytosiphon* are again found here in crevices.

The *Porphyra* association therefore extends from a foot above M.H.W.S. to M.H.W.N. and endures a wide range of exposure, varying from 99 to 60 per cent. of the total tidal period (Fig. 6). In the maximum region of growth (from +7 to +6 ft.) the thalli have an average exposure of 95 per cent. of the total tidal period and the continuous sheets of dry *Porphyra* plastered over the rock at this level and only to be peeled off with a knife, bear eloquent testimony to this. Probably the heavy gelatinous cell walls of the thallus are a protection, while the overlapping of the thalli serves to retain a certain amount of moisture. Johnson and Skutch (1928, II) have shown that after exposure at low water on bright days the proportion of moisture to dry weight may be as low as 13.8 per cent.



On the south, vertical face of the reef, *Porphyra* is not so plentiful either in numbers or extent, and in spite of the rough rock and the constant spray the spores do not germinate well here, or the sporelings do not survive. The thalli are only found in the central region (Table V) but the range is much the same as on the north face. Scattered plants of *Enteromorpha*, *Scytosiphon* and *Fucus spiralis* are again found associated.

The *Porphyra* association shows a definite seasonal occurrence. It appears first in the autumn (October to November) and is fertile throughout the winter. In April the formation is still well-developed. The fronds begin to die away in May and by early June only ragged and bleached remnants can be seen. During the summer months the rocks in the *Porphyra* zone remain bare, with only occasional dense patches of *Lichina pygmaea* and *Rivularia atra*. *Scytosiphon* and the other subdominant species of this region also die away and do not reappear until October. In what form the delicate spores of *Porphyra* pass the months from May to October is not known.

In general the position of this association at Peveril Point agrees with that at Clare Island (Cotton, 1912) and Loch Ine (Rees, 1935), though its upper level seems somewhat higher. It does not, however, correspond with the situation in the Faeroes where the lower limit is m.h.w. (Børgesen, 1905). In Norway Printz (1926) notes that the forma *laciniata* can extend down into the littoral region as far as m.l.w. and this agrees with the observations of Johnson and Skutch (1928, I) that although *Porphyra umbilicalis* occurred in the upper littoral at Mount Desert Island it was also the most widespread alga of the lower littoral regions. *P. umbilicalis* occurs in the region of the m.l.w.n. at Peveril Point though not in any great quantity, but this alga undoubtedly has the capacity of existing within the greatest possible range of exposure. A comparison of the character and physiological behaviour of the thalli from these two situations should throw much light on the constitution of the cell necessary to resist desiccation.

#### C. *Fucus spiralis* association.

*Fucus spiralis*, though again confined to definite limits, does not form so clear and well-marked an association as the species previously described. Where present as the dominant alga, it occupies an area either within or immediately below the lower limits of *Porphyra*. Two factors, apart from the limiting one of the amount of exposure which the alga can withstand, appear to reduce its incidence. First, the thallus favours a rough substratum and so flourishes best where there are numerous small creeks or pools; it can then become dominant even in so exposed a situation as the middle of the *Porphyra* area (in line 6). Indeed between +6.1 and +4.0 ft. *Porphyra* and *Fucus spiralis* are often competitive, though in the region of pools and creeks *Fucus* undoubtedly has the advantage. Secondly, the plants grow better in positions not subjected to too great a scour of the waves. Lines 4 and 5 are only

separated from one another by a few feet across a creek, but while scattered plants of *F. spiralis* are found in line 4 where the water sweeps violently through the creek, in the corresponding area of line 5 which is protected from the waves there is a dense growth (Fig. 5).

Table VI. *Distribution of Fucus spiralis on Reef II*

		Vertical height (ft.) above C.D.							
Lines ...	1 and 2	3	4	5	6	7	8	9	
North face	—	—	+5.5 to +4.5	+5.8 to +3.8	+6.1 to +4.9	+5.9 to +4.6	+4.9 to +3.2	+5.5 to +4.3	
South face	—	—	Scattered	—	—	—	Scattered	Scattered	

In Table VI the distribution of *F. spiralis* as measured on the reef is shown, and it will be seen that the range of growth of the species extends from 6.1 to 3.2 ft. above C.D., that is from M.H.W.S. almost to M.L.W.N. The association as a whole therefore has an average exposure ranging from 94 to 38 per cent. of the tidal period (Fig. 6). *F. spiralis* only grows in the region of M.L.W.N. in situations which are particularly sheltered; the maximum growth lies around M.H.W.N., and for a foot above, where the average exposure is 90-70 per cent. This corresponds almost exactly with the exposure limits of this species at Wembury (Coleman, 1933), not allowing for the splash zone in either case. Baker (1909) showed that in cultures the thalli grew better when exposed daily for 50 per cent. of the total period than when exposed for either 8 or 91 per cent., but she tested no intermediate exposures, and it seems probable that 70 or 80 per cent. exposure gives the most luxuriant growth. The form of the thallus differs considerably according to the amount of exposure undergone and in the region where *F. spiralis* is only exposed for 60 or 70 per cent. of the total period the thalli are considerably broader and better developed than when the exposure is above 80 per cent. of the total period.

On the south face of the reef, *F. spiralis* hardly appears at all except in the region of lines 8 and 9 where a horizontal shelf of rock juts out at 5.4 ft. above C.D. and *Fucus* is found sparsely scattered (Table VI).

*F. spiralis* persists upon the reef throughout the year and its upper and lower limits remain unaltered. In April the thalli were in good condition and fertile, and *Cladophora rupestris* and *Enteromorpha compressa* were growing freely among them. By June the plants were much shrivelled and dried up, while the associated algae had died away; in the lower part of the zone their place had been taken by a small and stunted development of *Nemalion multifidum*. This in turn died away by September when *Fucus spiralis* had somewhat recovered and was fertile, with swollen and gelatinous apices. Though not fertile through the winter months, it continued in good condition.

#### D. Bare zone.

Below the *Fucus spiralis* association there occurs a very conspicuous region to which the name of the bare zone has been given, for no algae grow here

with the exception of those that are found in the shallow rock pools and on the shells of limpets. In the pools in April there is a sparse flora consisting mainly of the following species:

*Cladophora rupestris*  
*Codium tomentosum*  
*Ulva lactuca*  
*Fucus serratus*  
*Corallina officinalis*

*Laurencia pinnatifida*  
*Gelidium latifolium*  
*Lomentaria articulata*  
*Polysiphonia Brodiaei*

And on the limpets are found:

*Enteromorpha intestinalis*  
*Scytosiphon lomentarius*

*Laurencia pinnatifida*

This region of bare rock has very sharply defined limits (Pl. XIX, phot. 2) and these are shown in Table VII.

Table VII. *Upper and lower boundaries of the bare zone on Reef II*

Lines ...	Vertical height (ft.) above c.d.								
	1	2	3	4	5	6	7	8	9
North face	—	+4.2 to +2.9	+4.0 to +2.6	+4.5 to +2.6	+3.8 to +2.0	+4.6 to +3.5	+4.5 to +2.7	—	—
South face	—	+4.5 to +3.5	+5.0 to +1.9	+5.8 to +1.9	+4.7 to +2.0	+4.3 to +3.0	+5.4 to +3.3	+4.5 to +1.9	+5.0 to +1.9

Thus on the north face of the reef, the bare zone extends from 4.6 to 2.0 ft. above c.d., that is from just above M.H.W.N. to (in one position) a foot below M.L.W.N. Usually, however, the lower limit lies at +2.6 ft., i.e. almost at M.L.W.N. The area thus has a range of exposure extending from 80 to 20 per cent. of the tidal period (Fig. 6).

The presence of the *bare zone* on the reefs at Peveril Point is perhaps the most peculiar feature of their algal ecology. The zone is so clearly defined and has such sharp limits that it would seem that some special factor must be preventing algal growth here. Yet the temperature, substratum, aspect and other conditions do not appear to differ in any way from those in the regions above or below. Since the exposure in this region is in no way excessive there seems to be no reason why *Fucus spiralis* should not spread down from above, as it can grow in situations with a minimum exposure of 40 per cent. (Fig. 5). Equally it would seem that the *Laurencia-Corallina* association might extend up from below, or the rock be colonised by some new association suited to the exposure of a mid-littoral situation.

Two reasons for this peculiarity are here suggested, both somewhat tentatively. It has already been shown that the region between 3 and 5 ft. above c.d. (i.e. between M.L.W.N. and a foot above M.H.W.N.) is the region where the maximum fluctuation in the periods of emergence and submergence occurs throughout the year (Fig. 4 and Table IV). Indeed a comparison between the highest spring tide of the year (July 29th) and the lowest neap tide (September 2nd) shows that the numbers of hours of exposure undergone in this region in a single tidal period of 12.5 hours may vary between 6.8 (springs) and 12.5

(neaps), a variation of approximately 54 per cent. This variability in the exposure period is greater than that undergone by the algae in any other region of the littoral area. Such great instability in the periods of emergence and submergence would mean that any alga colonising such an area would need to have a physiological constitution capable of adapting itself from day to day to widely different conditions of desiccation.

There is also another factor to be taken into consideration here. The rise or fall of the tide in any district does not continue evenly over the whole of the intertidal period. According to the Admiralty Manual of Navigation, during a 6-hour period of rise or fall, the tide covers half of the distance in the third and fourth hour, leaving the other half to be spread out over the remaining 4 hours. During the third and fourth hour of the tidal period at Peveril Point, the water is ebbing or flowing over the bare zone and this comparatively rapid movement may have something to do with the absence of vegetation here. This point has been mentioned by Elmhirst (1933) in connection with the distribution of Fucoid vegetation. He has shown that in the neighbourhood of the Millport Laboratory *Ascophyllum nodosum* occupies this middle region in sheltered positions and from a comparison of Coleman's chart (1933) the same is true of Wembury, where *Ascophyllum* grows in shelter in this region in uninterrupted sheets, only mingled below with *Fucus serratus*. In the sheltered places at Peveril Point, where considerable protection is offered by the curve of the bay, *Fucus serratus* may grow in this region (Table VI, lines 8 and 9), but for the most part the rocks are too exposed for this species, or for *Ascophyllum*, and since no other species has taken their place they remain bare.

On the south (vertical) face of the reef the bare zone is equally evident, having a greater upward range (Table VII). Since the sporelings of *Fucus spiralis* seem unable to develop on this vertical face the region that they might be expected to colonise is left vacant and forms an addition to the bare zone, thus accounting for its higher upper limit.

No algae invade the bare zone throughout the year. During the summer months the upper extension of the zone is added to in certain areas by the dying away of *Porphyra*, but apart from this the boundaries remain unchanged. *Scytosiphon* and *Enteromorpha* disappear almost entirely from the pools and limpets, and from June to September small and stunted plants of *Nemalion multifidum* are found on the rock. In the autumn the pools contain chiefly a fine growth of *Polysiphonia urceolata* and *P. macrocarpa*, together with *Enteromorpha marginata*.

#### E. *Ulva* association.

In the spring, a long green line bordering on the bare zone strikes the eye, and *Ulva lactuca* is found to be the dominant alga of this region. The thalli are small but are mainly fertile. A number of other algae are also found but

none of them occur in sufficient numbers at this time of the year to become serious rivals. The most frequent are:

<i>Cladophora rupestris</i>	<i>Corallina officinalis</i>
<i>Scytosiphon lomentarius</i>	<i>Gelidium latifolium</i>
<i>Fucus serratus</i> (scattered)	<i>Lomentaria articulata</i>
<i>Himanthalia lorea</i> (scattered)	<i>Chylocladia ovata</i>
<i>Porphyra umbilicalis</i> (broad form)	<i>Rhodymenia palmata</i>
<i>Laurencia pinnatifida</i>	<i>Gelidium pulchellum</i>
<i>Ceramium rubrum</i>	

Table VIII. *Distribution of the Ulva association on Reef II, April 1934*

Lines ...	Vertical height (ft.) above C.D.							
	1	2	3	4	5	6	7	8 and 9
North face	—	—	+2.6 to +1.6	+2.6 to +0.1	+2.0 to +0.5	+3.5 to +2.6	+2.7 to +0.1	—

The distribution of the *Ulva* association is shown in Table VIII and in Fig. 5, and it will be seen that the association extends from +3.5 to +0.1 ft. on the north side of the reef, that is from a foot above M.L.W.N. nearly to C.D. This involves an exposure range of 55–1 per cent. of the tidal period (Fig. 6). The maximum growth however is at M.L.W.N. and for about a foot below, where the exposure is from 20 to 7 per cent. of the tidal period. Here the thalli are larger and more luxuriant. Throughout the whole association the plants behave similarly to those of *Porphyra*. They reproduce in the winter and spring, and as the temperature rises in May the thalli are gradually killed off. A certain number of small plants remain, sheltered among the larger ones of *Laurencia* and *Corallina* in the lower part of the zone. By June, however, even these have almost disappeared and the dominant species is now *Leathesia difformis*, growing in such masses upon the other algae as to give a distinct brown coloration to the association. As additions to the subdominant flora listed above, *Pterosiphonia thuyoides*, *Phyllophora membranifolia* and *Laurencia obtusa* are found. By September the larger thalli of *Leathesia* have gone and the smaller ones which remain are no longer dominant. *Laurencia pinnatifida* and *Corallina officinalis* now assume this position; these species were present before but only in small quantities. A few scattered patches of *Ulva* can be seen and by December these have increased in number and size and *Ulva lactuca* is again the dominant alga. *Cladophora rupestris*, forming a green band in the lowest part of the association, persists throughout the year.

*Ulva*, as a dominant alga, does not appear to be common in this lower littoral region in other places. Johnson and Skutch (1928, I) note that it was present in this zone on Mount Desert Island in tide pools and sluices, but never in places where it could be uncovered for more than a few minutes. Printz (1926) found it on the west coast of Norway in the lower littoral and even in the sublittoral zone but always in sheltered places in the inner part of the fjord. Its abundance at Peveril Point may be due to the presence of the sewage pipe near by, though this does not wholly explain the distribution.

*Ulva* is absent from the reef in three regions. On the last 50 ft. (lines 1 and 2), where the scour of the waves is greatest, the vegetation is dominated by *Laurencia* and *Corallina* together with *Himanthalia* in large quantities. At the sheltered shoreward end (lines 8 and 9) the place of *Ulva* is taken by *Fucus serratus* and *F. vesiculosus* (Fig. 5). On the south face of the reef *Ulva* is not found at all.

This species therefore only attains dominance in the associations in regions which are neither too exposed nor too sheltered, and where the slope of the rock is such that the sporelings can obtain a foothold.

#### F. *Laurencia-Corallina* and *Himanthalia* association.

This association, represented by a dense low growth of *Laurencia pinnatifida*, some *L. obtusa*, *Corallina officinalis* and some *C. squamata*, extends over much the same range as *Ulva*, but is found in two of the regions where *Ulva* is absent, the rough and exposed seaward end and the vertical face where *Ulva* finds no foothold. This distribution is shown in Table IX and Fig. 5.

Table IX. *Distribution of Laurencia-Corallina and Himanthalia association on Reef II, April 1934*

		Vertical height (ft.) above C.D.							
Lines ...	1	2	3	4	5	6	7	8	9
North face	+3.0 to +1.5	+2.9 to +0.1	—	—	—	—	—	—	—
South face	Un- measured	+2.3 to +0.3	+2.0 to C.D.	+1.9 to C.D.	+2.1 to C.D.	+3.0 to C.D.	+3.3 to C.D.	+1.9 to C.D.	—

A number of other algae are found in this association: the commonest are the following:

*Cladophora rupestris* (lower part only)  
*Scytosiphon lomentarius*  
*Laminaria saccharina* (sporelings)  
*Chondrus crispus*  
*Pterosiphonia thuyoides*  
*P. parasitica*  
*Ceramium rubrum*  
*Polysiphonia fibrata*  
*Cryptopleura ramosum*  
*Polyneura Hilliae*

*Lomentaria ovalis*  
*Chylocladia articulata*  
*Griffithsia floeculosa*  
*Furcellaria fastigiata*  
*Callithamnion tetragonum*  
*Rhodymenia palmetta*  
*Plocamium coccineum*  
*Porphyra umbilicalis*  
*Rhodophyllis bifida*

It will be seen that this association extends from M.L.W.N. to C.D. and so has a maximum exposure of 30 per cent. of the tidal period.

This association has been noted in many localities but its constituents vary. At Clare Island it occurs in exactly the same position, from Mean Sea Level to Low Water (Cotton, 1912). On the very exposed rocks it takes the form of a *Corallina-Lithophyllum* association, *Corallina squamata* forming the bulk of the growth. In rather less open spots *Laurencia pinnatifida* and *Gigartina mamillosa* occupy this position, forming in the lower levels, as at Peveril Point, an undergrowth to *Himanthalia*. The associations at Lough Ine are similar (Rees, 1935). At Wembury no association is defined but *Gigartina stellata*

(=*G. mamillosa* J.G.Ag.) and *Chondrus crispus* are found in a comparable position, though their upper limits are rather lower. In other ecological accounts, so far as can be judged without measurements, it occurs regularly in the same position, the upper limit being near M.L.W.N. and the lower at C.D. or below. Printz (1926) notes that though not often found in the fjord he described on the west coast of Norway, yet when it does occur in any quantity it grows together with *Leathesia*, as at Peveril Point.

Both in position and constitution the *Laurencia-Corallina* association remains almost constant throughout the year. The dominant species are at their best during the spring and are then fertile. In the summer months *Laurencia* turns a yellow-green colour and *Corallina* is stunted and bleached. In the autumn they consist of young shoots, or older ones which are worn down and partially destroyed. Small patches of *Ulva* and *Leathesia* are found scattered among them, but these never develop to any great extent. Species additional to those listed make their appearance in June, the principal ones being *Nemalion multifidum*, *Polysiphonia urceolata*, *Ceramium echinotum* and *Callithamnion Hookeri*; but these do little to alter the general appearance or constitution of the association.

*Himanthalia lorea* also occurs in this association at the far end of Reef II, extending from +2.0 ft. to C.D., i.e. with an average exposure of 10 per cent. of the tidal period or less (Figs. 5 and 6). In the upper part of this region, at a very low spring tide, the plants may be exposed continuously for as much as 3.6 hours, or 29 per cent. of the tidal period, but although this is exceptional it is not surprising that the thalli here are scattered and stunted. Lower down the fertile thalli grow luxuriantly, with the *Laurencia-Corallina* association as undergrowth. *Himanthalia* is believed to welcome rough water, but on the south vertical wall, where the waves break with much force, the plants are few and scattered. *Himanthalia* is found scattered on many boulders at or below low water, but not in any great amount, and the almost complete submergence of the boulders may account for this. The spores, which seem to germinate at all times of the year, apparently prefer a region where they are neither completely submerged nor subjected to too great a scour of the water.

One other species is found associated with the *Laurencia-Corallina* association in such profusion as to become dominant between +1.7 and -0.1 ft. on the last 20 ft. of the reef—*Calliblepharis lanceolata*. It grows in this region with *Furcellaria fastigiata*, while *Laurencia* and *Corallina* occur as an undergrowth. A few scattered plants of *Calliblepharis* are also found on the vertical face of the reef.

#### G. *Fucus serratus* association.

*Fucus serratus* forms a very definite association on the north side of Reef II, occupying a position below the *Ulva* association. It constitutes a wedge-shaped area. For about 70 ft. from the seaward end of the reef it is

absent and then it starts as a narrow region, intermixed with *Laminaria digitata* at the lower levels and gradually broadening out towards the landward end (Table X, Fig. 5).

Table X. *Distribution of the Fucus serratus association on Reef II*

		Vertical height (ft.) above C.D.							
Lines ...	1 and 2	3	4	5	6	7	8	9	
North face	—	+1.2 to +0.7	+1.0 to C.D.	+0.7 to C.D.	+2.6 to +1.0	+2.7 to C.D.	+3.2 to +1.2	+3.6 to +2.3	

The maximum range of this association is therefore from +3.6 ft. to C.D., i.e. with an upper limit lying between M.H.W.N. and M.L.W.N. and a lower limit at low water. It has a range of exposure varying between 52 and 0 per cent. of the total tidal period (Fig. 6). The maximum exposure is found on the sheltered landward end of the reef (Fig. 5), and in less sheltered places the greatest exposure is only about 14 per cent. of the tidal period, while in rough situations this association is replaced by the *Laurencia-Corallina* and the *Laminaria* associations. The position which this *Fucus serratus* association holds seems to correspond with that in other localities, and the degree of exposure to which it is subjected agrees very closely with that at Wembury (Coleman, 1933) where *F. serratus* is subject to exposure ranging from 50 to 0 per cent., not allowing for the splash zone in either case.

The following species are associated with *F. serratus*:

<i>Cladophora rupestris</i>	<i>Corallina officinalis</i>
<i>C. arcta</i>	<i>Lomentaria ovalis</i>
<i>Porphyra umbilicalis</i> (epiphytic on <i>Fucus</i> )	<i>Melobesia speciosa</i>
<i>Laurencia pinnatifida</i>	<i>Polysiphonia nigrescens</i>
<i>Rhodymenia palmata</i> (in large quantities)	<i>Chondrus crispus</i>
<i>Ceramium rubrum</i> (epiphytic on <i>Fucus</i> )	<i>Chylocladia ovata</i>
<i>C. echinotum</i>	

In addition *F. vesiculosus* is present, but only in the sheltered regions of the landward end of the reef. Here it forms the dominant alga over an area extending from +3.6 to +2.3 ft. above C.D. and *F. serratus* is not present. Below this level the two species are mixed.

*Fucus serratus* decreases in quantity towards the summer. In June the plants have become worn down and are scattered in patches. By September the thalli have partially recovered and show signs of development of fertile conceptacles. They are accompanied at this season mainly by *Ceramium rubrum* and *Rhodymenia palmata*, but the last-named species, which was abundant in April, has now become partially decayed and eaten and is overloaded with epiphytes. *Fucus serratus* is fully fertile by December.

*F. vesiculosus* withstands the summer heat better than *F. serratus*. By June it has become dominant over *F. serratus* and in September it is still holding its own and is in a healthy condition, some plants being fertile. But as the plants of *F. serratus* rise to dominance, become more luxuriant in



growth and increase in numbers in the winter months, *F. vesiculosus* decreases in amount.

#### H. *The Laminaria association.*

The chief region of dominance of the species of *Laminaria* is of course below Low-Water Mark, but they must be included here among the littoral algae because in certain situations they become dominant above this level. *Laminaria digitata* is the principal member of this association, and the distribution of this species on the last 70 ft. of the reef is shown in Table XI and Fig. 5.

Table XI. *Distribution of the Laminaria association on Reef II*

		Vertical height (ft.) above C.D.					
Lines ...	1 and 2	3	4	5	6	7	8 and 9
North face	Below M.L.W.	+1.2 to below C.D.	+1.2 to below C.D.	+0.7 to below C.D.	Below C.D.		—
South face	„	+1.0 to below C.D.	Below C.D.	+1.2 to below C.D.	+1.2 to below C.D.		—

The association extends on the north face from 1.2 ft. above C.D. into the submerged zone and on an average is never subjected to a greater exposure than 5 per cent. of the total tidal period (Fig. 6). During low spring tides the upper part of the *Laminaria* zone may be laid bare for nearly 2 hours continuously, that is to say 16 per cent. of the tidal period, but during an average tide the upper part of the association is not exposed for more than 40 min. continuously, while during the intervening neap tides it is never exposed. This general position for the *Laminaria* association is well known on all exposed coasts.

*Laminaria digitata* is associated with some *L. saccharina*, *L. Cloustoni* with *Rhodymenia palmata* growing on the rough stipe, *Fucus serratus* and *Chondrus crispus*. Though the upper plants are smaller than those around C.D., *Laminaria Cloustoni* grows to a considerable size at M.L.W.N. Below this there is a large and flourishing growth mainly of *L. digitata* and *L. saccharina*. On the south, vertical face, *L. digitata* is found up to 1.5 ft. above C.D.

The *Laminaria* association tends to be restricted in its upper levels during the summer months, but otherwise shows little variation in position.

#### *Summary of the associations.*

It will be seen from this description that eight marine algal associations occur in the littoral region on Reef II at Peveril Point and their vertical extent on the north face of the reef is summarised in Table XII and in Fig. 6.

An investigation was also made of the algal associations of Reef I and of their relation to the periods of emergence and submergence in order to ascertain the effect of a change in slope upon the distribution and periodicity.

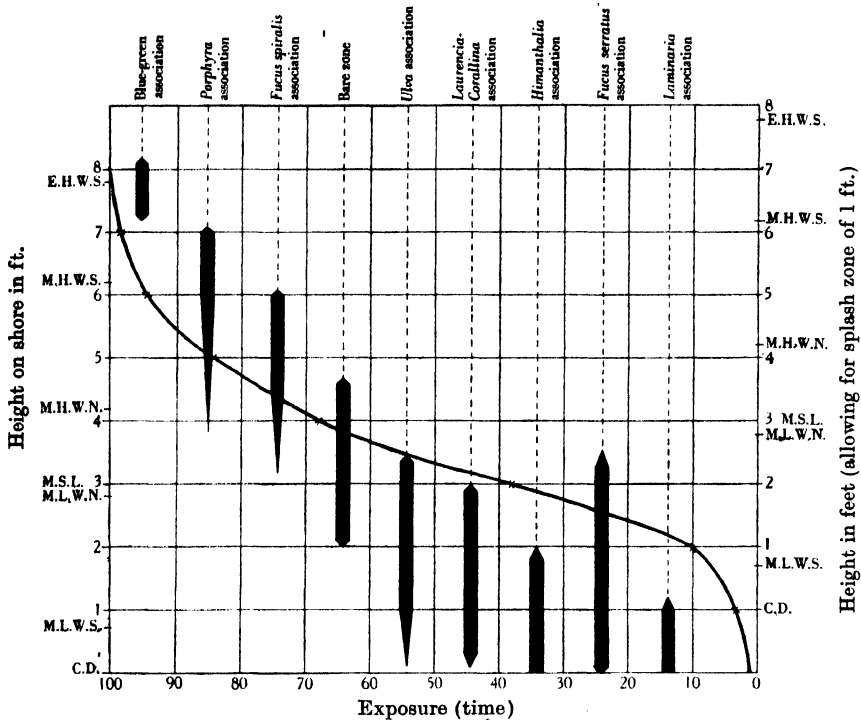


FIG. 6. The vertical distribution of eight littoral associations showing their upper and lower limits on the reefs at Peveril Point. The vertical heights above C.D. in the left-hand column are raised by 1 ft. in the right-hand column to allow for a 1-ft. splash zone. The curve shows the average percentage exposure, based on the four fortnights, at different heights above C.D. See Table IV, Column IV, p. 401.

Table XII. Vertical range and percentage period of exposure undergone by eight algal associations on Reef II together with the maximum regions of growth and their exposure

Main dominants of associations	Upper and lower limits (ft. above C.D.)	Period of emergence %	Region of maximum growth	Period of emergence %
A. Blue-green algae	8.2 to 7.2	100	Same	Same
B. <i>Porphyra</i>	7.1 to 3.8	99 to 60	7.1 to 6.0	99 to 94
C. <i>Fucus spiralis</i>	6.1 to 3.2	94 to 38	5.5 to 4.5	89 to 75.5
D. Bare zone	4.6 to 2.0	77 to 10	4.6 to 3.0	75.5 to 30.8
E. <i>Ulva</i>	3.5 to C.D.	49 to 1	2.6 to 1.6	22.5 to 7.0
F. <i>Laurencia-Corallina</i>	3.0 to C.D.	31 to 1	2.0 to 1.5	10 to 6.7
G. <i>Fucus serratus</i>	3.6 to C.D.	52 to 1	2.2 to C.D.	14 to 1
H. <i>Laminaria</i>	1.2 to below C.D.	4.6 to 0	Same	Same

#### COMPARISON OF THE ALGAL ASSOCIATIONS OF REEF I WITH THOSE OF REEF II

Reef I runs parallel to Reef II, some 200 ft. to the north of it (Fig. 2). The two reefs are similar in geological structure, but owing to synclinal folding

they slope in opposite directions. On Reef I the northern face is the vertical one and the southern slopes at an angle of approximately 70° from the vertical. The northern face is to some extent protected by a sewage pipe which runs far out to sea, parallel but some 20 ft. north of it; vegetation grows over this and boulders have collected between it and the reef, breaking the force of the current. At about 85 ft. from the landward end the reef is broken by a large cleft (Fig. 2). Five traverses or lines were chosen and levelled in the second part of the reef beyond the cleft, and observations and measurements were made more particularly along these lines, that is at an average distance apart of 36 ft. (Table I). The following notes are not intended as a complete description of the reef but as a comparison showing the similarities and differences between the associations of Reefs I and II (see throughout Fig. 7).

#### A. *Blue-green association*

As a dominant *Rivularia atra* is absent, probably because on this reef the highest point is +7.3 ft. and this species grows best above that level. Occasional patches were found in September and also patches of *Lichina pygmaea*.

#### B. *Porphyra association*

From October to May this extends the whole length of the surveyed area with the exception of the last 30 ft. which fall below the lower limit for this species (Fig. 7). On the sloping (southern) face the association has a range extending from +7.3 to +4.0 ft. and this corresponds to a similar range and exposure on Reef II. On the northern face *Porphyra* is sparse, being abundant only around line 4 where the vertical drop is broken at 1.3 ft. below the crest of the ridge by a horizontal shelf. A certain amount of *Enteromorpha intestinalis* and *Scytosiphon lomentarius* grow in the zone, more particularly in pools and on limpets. Scattered plants of *F. spiralis* are also found but not in such numbers as on Reef II. *Porphyra* therefore will grow in abundance on a limestone reef with either a northern or a southern aspect, so long as some slight protection is afforded by the slope of the rock. But if the substratum is vertical the spores seem to have difficulty in making a secure attachment, probably owing to the force of the waves.

#### C. *Fucus spiralis association*

As a dominant alga, *F. spiralis* does not occur at all on Reef I. On the other reef this species flourishes best on the sloping northern face and in positions which are sheltered from excessive insolation. On Reef I the northern face is vertical while the sloping southern face is well exposed to the sun. As a result *F. spiralis* is completely absent except in pools. The position that, by comparison with Reef I, it would be expected to occupy (between +6.0 and +3.2 ft.) is here either taken up by *Porphyra* or it remains bare rock.

D. *Bare zone*

The bare zone is well marked on Reef I on both the vertical and sloping faces. It extends the full length of the area surveyed with the exception of the last 30 ft. (Fig. 7). On the southern face it has a lower limit similar to that on Reef II, while (owing to the absence of *F. spiralis*) there is a higher upper limit (+6.1 ft.). The range of exposure of this zone is therefore much greater than on Reef II and a southern aspect decreases the possibility of algal growth in this mid-littoral region. On the northern vertical face the bare zone has also considerably extended its area and reaches up to +7.5 ft. Apart from the occasional pools and limpets with algae growing in or on them, similar to those of Reef II, no species are found in this zone.

(E) *Ulva* and (F) *Laurencia-Corallina* associations

One of the most striking differences between the two reefs is the combination of the two zones *E* and *F* into one on Reef I. Here, looking along the sloping southern face at low water in April, there is no long green line of *Ulva* to be seen below the bare zone. In its place there is a reddish brown band with a greenish tinge below. This is the *Laurencia-Corallina* association including relatively little *Ulva*, and with *Cladophora rupestris* growing in large quantities at the lower limit (Fig. 7).

The dominance or otherwise of *Ulva lactuca* seems connected with the slope and aspect. This species prefers sloping or creviced rock in a situation that is not too exposed. It grows but sparsely on a vertical face whether the aspect is north (Reef I) or south (Reef II). On a sloping substratum it favours a northern aspect (Reef II) rather than a southern one (Reef I). Its region of growth in the littoral area roughly corresponds with that of the *Laurencia-Corallina* association. In a favourable situation (sloping substratum, northern aspect, i.e. on Reef II), it grows in great profusion in winter and spring and easily becomes dominant; *Laurencia* and *Corallina* are then subdominant. In a semi-favourable region (sloping substratum, southern aspect, i.e. on Reef I), *Ulva* is subdominant to *Laurencia* and *Corallina*. In an unfavourable situation (vertical wall and either northern or southern aspect, i.e. on Reefs I and II), it only occurs scattered, and *Laurencia* and *Corallina* are completely dominant. Its rarity on the northern vertical wall of Reef I is all the more striking since the sewage pipe runs parallel with this face some 20 ft. distant, and the presence of organic matter is believed to promote the growth of *Ulva* (cf. Cotton, 1911).

The conclusion appears to be that even when other conditions such as substratum and slope are favourable, *Ulva* will not grow in this lower littoral region when subjected to the complex effects of too strong insolation. This is borne out by the fact that on flat or southward-facing coasts this species is often found in sheltered tidal pools near M.L.W. while it does not grow in any

quantity upon the open shore. Cotton (1912) found it in the rock pools of Clare Island as a dominant in August and September, though it is not mentioned among the associations of the coast formation, and Rees (1935) notes that it becomes dominant below the *Ascophyllum* association, but only on sheltered coasts.

The *Laurencia-Corallina* association occurs on both faces of Reef I, on the southern face from +4.7 to +0.9 ft., and on the northern face from +4.6 ft. to Chart Datum. The area occupied and the exposure correspond as a whole with that on Reef II, while the algae associated with the dominants are similar to those found in this association on Reef II. *Himanthalia lorea*, which was found in large quantities on Reef II, is absent here, while *Calliblepharis lanceolata* is only met with as scattered plants. The reason for this is not clear, since the tidal exposure and the action of the waves are approximately similar to those of Reef II. Børgesen (1905) noted that *Himanthalia* cannot withstand any appreciable amount of desiccation and Fischer-Piette (1932) has advanced reasons for believing that this species is highly susceptible to the effects of insolation, only growing in certain light intensities. This may account for its absence in situations with a southern aspect, as in this case.

#### G. *Fucus serratus* association

Following on the *Laurencia-Corallina* association, on the southern slope, there is a very definite region with *F. serratus* as the dominant alga. Towards the landward end of the reef this association widens until it extends from +2.9 to -0.3 ft. (Fig. 7). Thus the maximum and minimum limits are lower than on Reef II, and the range of exposure somewhat less, extending from 35 to 0 per cent. of the tidal period. *F. serratus* also occurs on the lower part of the northern face, but its position here is to some extent a sheltered one owing to the many boulders which lie scattered at the base of the reef on this side. The chief associated algae are similar to those on Reef II. *Rhodymenia palmata* is by far the most abundant, occurring in large quantities towards the lower part of the area, particularly on the southern face. *Chondrus crispus* is also common. *Fucus vesiculosus* is found only as scattered plants occurring in pools and creeks.

#### *Comparison of the Fucus associations with those of other coasts*

The associations of Fucaceae on the reefs at Peveril Point are dominated by the four species: *F. spiralis*, *F. vesiculosus*, *F. serratus*, and *Himanthalia lorea*. *Pelvetia canaliculata* and *Ascophyllum nodosum*, which are commonly present in other regions (Clare Island, Port Erin, Faeroes, etc.), are absent here. *Pelvetia canaliculata* grows at Clare Island "just above the ordinary high water level" on exposed coasts, though at Church Reef, Plymouth, it has a lower distribution and occurs down to extreme high water neaps. Its absence on the reefs at Peveril Point may be due partly to the fact that the

ridge only rises above the high water level in a few places. The shore itself is low and sloping and covered with boulders and *Pelvetia* is absent. *Ascophyllum nodosum* is a species which requires shelter and it is found on the inner, or sheltered side of the boulders scattered on the shore at Peveril Point. On the reefs it does not occur at all since there is little shelter to be found.

The sequence of those members of the Fucaceae which do occur here agrees well with that described for other parts of the south English coast and for Clare Island.

#### H. *Laminaria* association

The *Fucus serratus* association grades into the *Laminaria* association without any definite break between the two. At both ends of the observed area of the reef *Laminaria digitata* can be found growing as high as +1.2 ft., i.e. in a similar position and with similar exposure to that on Reef II (Fig. 7). Associated with this species is a more varied flora than on Reef II, including the following:

<i>Cladophora rupestris</i>	<i>Callithamnion tetragonum</i> (epiphytic on <i>Laminaria digitata</i> )
<i>Laminaria saccharina</i> (at low water and below)	<i>Plumaria elegans</i>
<i>Chondrus crispus</i>	<i>Griffithsia floeculosa</i>
<i>Corallina officinalis</i>	<i>Polysiphonia fibrata</i>
<i>Rhodomenia palmata</i> (in large quantities)	<i>Gelidium latifolium</i>
<i>Laurencia pinnatifida</i>	
<i>Lomentaria ovalis</i>	

Table XIII. *A comparison of the vertical distribution (ft. above C.D.) of eight algal associations on Reefs I and II, Peveril Point*

Association	Reef I, southern slope	Reef II, northern slope
A. Blue-green	—	+8.5 to +7.2
B. <i>Porphyra</i>	+7.3 to +4.0	+7.1 to +3.8
C. <i>Fucus spiralis</i>	—	+6.1 to +3.2
D. Bare zone	+6.1 to +2.6	+4.6 to +2.0
E. <i>Ulva</i>	—	+3.5 to +0.1
F. <i>Laurencia-Corallina</i>	+4.7 to +0.9	+3.0 to +0.1
G. <i>Fucus serratus</i>	+2.9 to -0.3	+3.6 to C.D.
H. <i>Laminaria</i>	+1.2 to below C.D.	+1.2 to below C.D.

#### *Conclusions on the algal distribution on Reefs I and II*

Eight associations are found on the northern slope of Reef II, but only five are present on the southern slope of Reef I. Of the three which are missing, one, the blue-green association, can be accounted for, as Reef I only rises to about a foot above M.H.W.S. and the association grows best above that level. The other two absent associations are those dominated by *Fucus spiralis* and *Ulva lactuca* respectively, and it is impossible to avoid the conclusion that since other conditions, such as substratum, periods of emergence, and exposure to wave action, are closely similar in both situations, these absences are related to the variation in aspect in the two reefs, and the increased insolation on the southern face of Reef I. Other striking absentees are *Fucus vesiculosus*, *Himantalia lorea* and *Calliblepharis lanceolata*. Other things being equal, the first two of these are believed to prefer situations which are not too greatly

exposed to the effects of light and consequent desiccation, and this would explain their absence in this southern aspect. The observations made here of certain omissions from the flora on the southern face of Reef I support the remark of Rees (1935) that, at Loch Ine, the south facing aspects of the inlets have on the whole a poorer vegetation than the slopes facing north.

Allowing for the absence of the *Fucus spiralis* and *Ulva lactuca* associations the ranges of the remaining five associations on Reef I do not show any wide variations from those on Reef II, and the periods of exposure to which the algae are subject remain approximately constant. The bare zone extends higher than on Reef I, owing to the absence of the *Fucus spiralis* association above it, and the *Laurencia-Corallina* association is not dominated by *Ulva* in its upper region. Apart from these exceptions the associations do not seem affected by the increased insolation and bear the same relation to the periods of emergence and submergence as on the north face of Reef II.

#### CONCLUSION

It has long been known that there is a definite sequence of algal associations in the littoral region of the shore. On many coasts the boundaries of the associations are not so sharply delimited as they are in the case of the eight described here and one type of vegetation grades into another. Yet it has frequently been observed that there are definite limits above or below which an association will not flourish.

Among the many problems encountered in the course of this investigation, perhaps none is more outstanding than the sharp delimitation of one zone from another at Peveril Point, particularly on the borders of the bare zone. The *Porphyra* plants fail to stray down on to the bare rock region and *Ulva* and *Corallina* do not wander up beyond their line of demarcation. At Wembury "these sharp boundaries only occur on the upper parts of the shore" (Coleman, 1933), but at Peveril Point they are found throughout the whole littoral region. Gail (1920) and Atkins (1922) have shown that the thalli and spores of *Fucus* and plants of *Ceramium* only grow within a certain range of hydrogen-ion concentration and if this is exceeded the plants die or there is little growth of the sporelings. This may possibly throw some light on why one association does not penetrate another, since the algae or fauna of one association may so raise or lower the pH of the sea water in their vicinity during the periods of emergence, that the environment is unsuitable for the growth of the algae of another association. Possible as this explanation is, it still does not make clear the reason for the strict delimitation of the boundaries where the associations border on the bare zone, and no solution of this problem is at present in sight.

In this paper the boundaries of the associations have been defined in terms of emergence and submergence, each association having a larger or smaller range of exposure which it will not exceed. The methods employed in ascer-

taining the exposure are not new, though they have been rarely used. They were originated and applied by Johnson and York (1915) in an examination of the littoral vegetation of Cold Spring Harbour and were used again by Johnson and Skutch (1928, I) on the littoral and tide-pool vegetation at Mount Desert Island. In this country Coleman (1933) has made use of them in the study of marine zonation at Wembury. Although there are so few data available for comparison, yet this attempt at Peveril Point to obtain more precise knowledge of the algal zonation in one region of the British Isles has brought to light the striking fact that in two widely separated areas, Wembury and Durlston Bay, both exposed, but with different substrata, different slopes of the rock, widely differing tidal ranges and possibly different temperature and illumination, the periods of emergence and submergence tolerated by the species investigated are precisely similar. Only three of the eight algal species studied by Coleman occur in any quantity at Peveril Point (*Fucus spiralis*, *F. serratus* and *Laminaria digitata*), and their vertical ranges correspond exactly in the two localities. In other words, these littoral algae only grow in that position on the shore in which they find those conditions of emergence and submergence to which they are adapted. It seems more than probable from such data as are available that this is true of many species in many different localities.

It is not suggested that the *average* period of exposure, either over a day, a fortnight or a longer time represents the only critical factor in the determination of germination or survival in a particular area. Undoubtedly at the lower levels of the shore the exceptional periods of exposure which occur occasionally at the low spring tides must play a very important part in determining this. During 1934 the lowest spring tide at Peveril Point was on the morning of July 29th, when at M.L.W.S. the algae which are normally rarely exposed at all or only for a few minutes, lay bare for 2 hours continuously, while down to nearly a foot below C.D. the exposure was from 30 min. to 2 hours. We have at present no means of estimating the effects of such a prolonged period of exposure and consequent desiccation upon spores and thalli accustomed to complete submergence, but undoubtedly it must involve death in some cases and considerable physiological changes in others, especially as these exceptional tides generally occur during the warmer months of the year.

Spring tides with so great a range do not increase the exposure in the middle and upper tidal regions but rather diminish it. The period of emergence in these regions is increased at the time of the extreme (lowest) neap tides when, at Peveril Point, owing to the small tidal range, the water rises and falls only a foot or less. Such a tide occurred on September 2nd, when for 24 hours the water remained almost stationary between M.H.W.N. and M.L.W.N. All levels above this suffered 24 hours' continuous exposure. As this happened to be a calm day there was little spray to fall on these upper levels and the desiccation must have been unusually severe.



Other factors, apart from the direct effects of the desiccation brought on by periods of emergence, are of course involved in the determination of the zonation of any particular species, for temperature and insolation can act as limiting agents, particularly in the lower regions of the shore, while shelter and the nature of the substratum give rise to marked modifications. It is evident, however, that among these interacting factors, the duration of the periods of emergence and submergence must be regarded as of primary importance.

#### SUMMARY

1. An investigation has been made of the marine littoral vegetation at Peveril Point, Dorset, with a view to ascertaining the sequence and range of the algal associations and their relation to the tidal flow.

2. The two main reefs of rock in this district have been measured and surveyed and by means of observations throughout a year the vertical height of the algal associations above "Chart Datum", i.e. a plane below which the tide seldom falls, has been ascertained. It was found that on the sloping rocks facing north there are eight distinct associations (see Table XII and Fig. 6 for a summary of these). On the sloping rocks facing south three are absent, the blue-green, *Fucus spiralis* and *Ulva* associations, and this is accounted for by the increased insolation. On the vertical faces of the rocks, whether facing north or south, the associations are very sparsely developed.

3. The average amount of exposure undergone by each association has been calculated and it was found that each dominant algal species has a very definite range of exposure above or below which it does not flourish successfully. Within this there is a limited range of exposure at which growth is most luxuriant (see Table XII for a summary of these exposures). The extent of an association is therefore limited by the capacity of the dominant species to endure a certain limited range of exposure, and it will not grow in regions where the exposure is greater or less.

4. Only one other investigation has been carried out on these lines on the coasts of Great Britain, that of Coleman at Wembury (1933). Three of the species which he investigated occur as dominant algae at Peveril Point, *Fucus spiralis*, *F. serratus* and *Laminaria*, and it is found that their range of exposure is almost exactly similar in these two widely separated areas.

5. The problem of the bare zone which occurs between the *Fucus spiralis* and *Laurencia-Corallina* associations is considered. No algae grow here. Calculations show that in this region (between M.H.W.N. and M.L.W.N.) the tide falls or rises more rapidly than at either higher or lower levels of the shore. Also the fluctuation in the periods of exposure undergone at different periods of the year is greater here than at other levels of the shore and it is suggested that these two causes may account for the lack of vegetation in this region. The very sharp boundaries delimiting one association from another, particu-

larly on the borders of the bare zone, are also considered, but no satisfactory reasons for this phenomenon can be advanced at present.

6. The conclusion is reached that, among many interacting factors, emergence and submergence are of primary importance in the determination of the position and extent of algal associations in the littoral area.

## REFERENCES

- Atkins, W. R. G. "The influence upon algal cells of an alteration in the pH concentration of sea water." *J. Mar. Biol. Ass. U.K.* **12**, 1922.
- Baker, S. M. "Causes of zoning of brown seaweeds on the seashore." *New Phytol.* **8**, 1909.
- Børgesen, F. "The Algae-Vegetation of the Faerøese Coasts." *Botany of the Faerøes*, Part 2, 1905.
- Coleman, J. "Nature of intertidal zonation of plants and animals." *J. Mar. Biol. Ass. U.K.* **18**, 1933.
- Cotton, A. D. "On the growth of *Ulva latissima*... with special reference to Belfast Lough." *Bot. Rep. Roy. Comm. Sewage Disposal*, 7th Report, pp. 121-42, 1911.
- Cotton, A. D. "Clare Island Survey." *Proc. R. Irish Acad.* **31**, 1, Pt 15, 1-178, 1912.
- Elmhirst, R. "Tidal flow and littoral zonation." *Scot. Mar. Biol. Ass. Ann. Report*, pp. 12-15, 1933.
- Fischer-Piette, E. "Répartition des principales espèces... des côtes et des îles de la Manche." *Ann. Inst. Oceanographique*, **12**, Fasc. 4, 1932.
- Gail, F. W. "pH concentration and other factors affecting the distribution of *Fucus*." *Publ. Puget Sd Biol. Stat.* **2**, 1920.
- Johnson, D. S. and Skutch, A. F. "Littoral vegetation on a headland of Mount Desert Island. I. Submersible or strictly littoral vegetation. II. Tide pools and the environment." *Ecology*, **9**, 2 and 3, 1928.
- Johnson, D. S. and York, H. H. "The relation of plants to tide levels." *Publ. Carneg. Instn.*, No. 206, Washington, 1915.
- Printz, H. "Algenvegetation of Trondhjemsfjordes." *Skrift. Norske VidenskAkad. Naturvidensk.* **5**, 1-274, 1926.
- Rees, T. K. "The marine algae of Lough Ine." *This JOURN.* **23**, 1, 1935.

# THE LAND VEGETATION OF AILSA CRAIG

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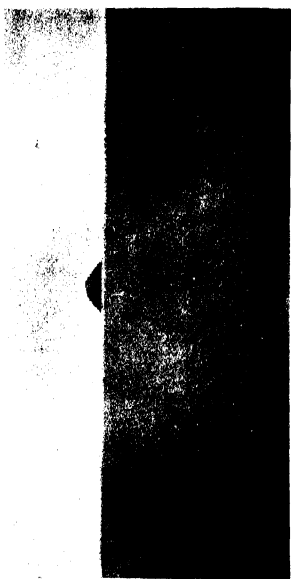
(*With Plates XX-XXIII and nine Figures in the Text*)

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IN this study an attempt has been made to produce for the first time a description of the physiographic factors and resulting vegetation on the rock of Ailsa Craig, and to draw up a scheme indicating the limited amount of succession taking place. Previous botanists have made lists of the plants and their results are summarised at the end. I have spent a considerable time on the rock during the years from 1930 onwards, but the main work was carried out in August 1934, and during the spring and summer of 1935.





Phot. 1. Ailsa Craig, seen from Bannane Head,  
Ayrshire.



Phot. 2. Ailsa Craig from 3 miles east.



Phot. 3. Pier and sea during the storm of April 10th, 1934,  
to show vortices of sea spray.



Phot. 4. View looking south from near lighthouse on east  
side of Ailsa Craig, showing heather slopes to the right.

VEVERS—VEGETATION OF AILSA CRAIG

I am much indebted to Mr McGaw, Principal of the Ailsa Craig Lighthouse, for the readings of temperature and rainfall for 1934; and to Mr M. Girvan, Mr James Girvan, and Captain A. Girvan for their assistance on the Craig itself; to Mr Sherrin and Mr I. M. Lamb (of the Department of Botany, British Museum) for their help in naming and verifying many of the Bryophytes and Lichens; and especially to Prof. Tansley for the trouble he has taken in reading and criticising the script of the paper.

## INTRODUCTION

### POSITION AND TOPOGRAPHY

Ailsa Craig is situated in the Firth of Clyde in latitude  $55^{\circ} 15' N.$  and longitude  $5^{\circ} 6' W.$  The nearest part of the mainland is Ardwell Point,  $8\frac{1}{2}$  miles to the south-east: Girvan is  $9\frac{1}{2}$  miles east-south-east. Pladda in Arran is 12 miles distant, Corsewall Point in Wigtownshire 17 miles, and the nearest part of Ireland 36 miles.

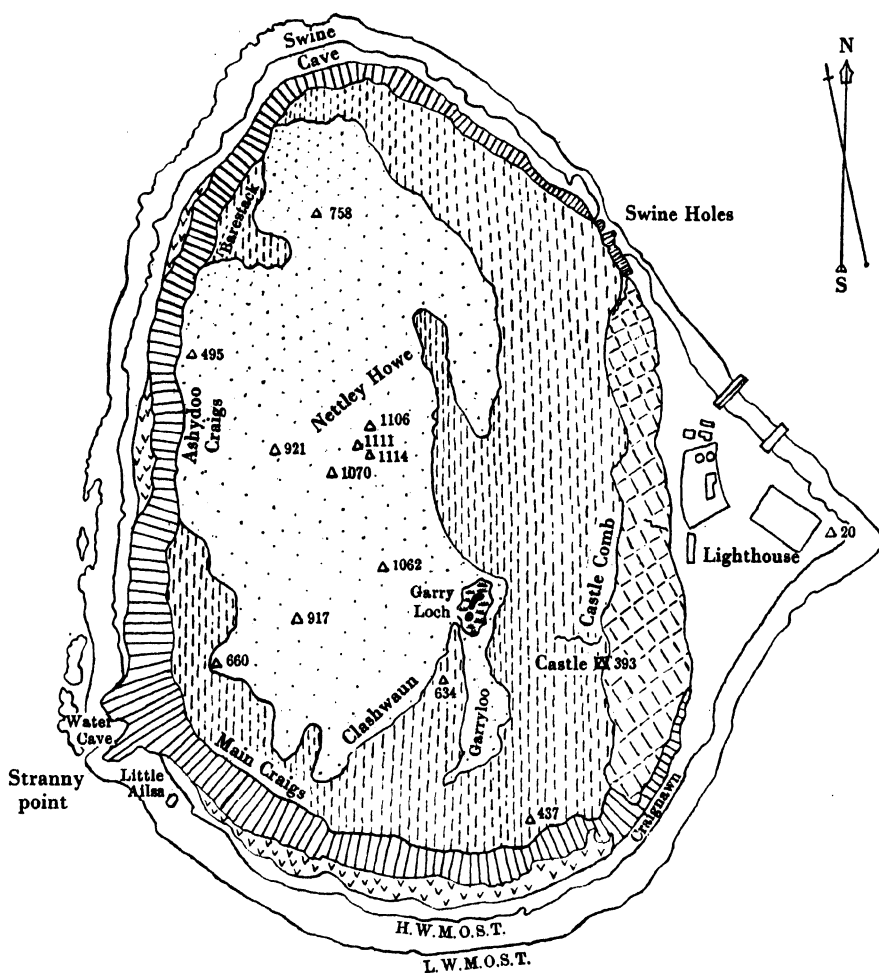
According to the measurements of the Ordnance Survey the Craig is 3900 ft. in length, 2600 ft. in breadth and 1114 ft. in height. In circumference it is rather more than  $2\frac{1}{4}$  miles, and it covers an area of 224·951 acres (Fig. 1). The best approximation of the main outline of a vertical section from north to south can be obtained from a photograph of the rock from Girvan; similarly of the section north-north-west—south-south-east in the view looking north-north-west from the Bay of Ballantrae (Pl. XX, phot. 1).

On the north, south and west sides the rock rises abruptly from sea-level to about 700 ft., either by perpendicular cliffs or very steep screes. The highest cliff is the Barestack (600 ft. approx.). On the east side the rock is not quite so steep, but even here the average angle of the slope is  $40^{\circ}$ , and the slope from the Castle straight down to sea-level has an angle of  $51^{\circ}$ , that is, a gradient of 1 in 0·3.

The surface of the rock is broken up by the various "howes" or "loos" as the natives call them. The largest of these are Nettley Howe, Clashwaun and Garryloo, and there are also numerous small openings in the cliffs which are in most cases actual gaps in the granite, once occupied by the intrusive dolerite dykes, and forming a natural drainage system for those parts in which they occur.

### CLIMATIC FACTORS

The climate may be described as an extreme form of that found in the rest of the Clyde area, this being due to the lack of shelter and to the exposed nature of the whole rock. The prevailing winds throughout the greater part of the year are south to south-west. Owing to the shape of the rock these winds affect all parts except the caves and clefts; for they blow round both the east and the west sides, meeting in the north and north-east where the



SCALE: Six inches to one mile=1:10560.

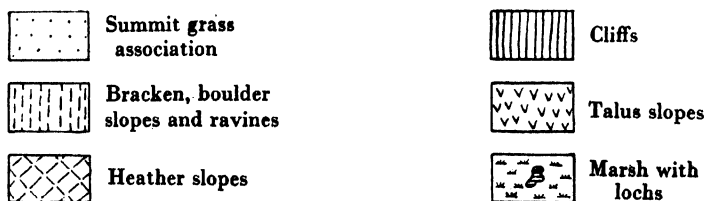


FIG. 1. Vegetation chart of Ailsa Craig.

sea spray is gathered up by them into a series of vortices, which may travel for over  $\frac{1}{4}$  mile (Fig. 2 and Pl. XX, phot. 3).

Rainfall records are available only for the last 4 years (1932-5) and include the exceptionally dry year 1933, so that the average for the 4 years (30.78 in.) is probably below the mean. The annual totals were: for 1932, 37.52 in.; for 1933, 22 in.; for 1934, 33.28 in.; for 1935, 30.34 in.

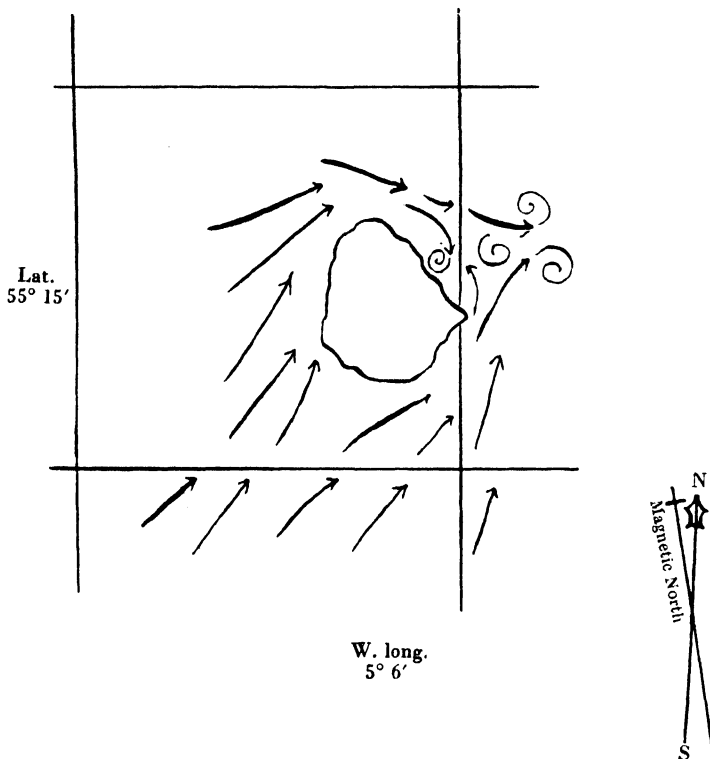


FIG. 2. Showing prevailing south-west winds on Ailsa Craig, and their effect in producing vortices.

The graph (Fig. 3) shows a flat low level in spring and summer, probably too low because of the unusually dry summers of the 4-year period, and a marked autumn maximum. The November average is probably too low owing to the very low rainfall (0.79 in.) of November 1934.

The temperature graph (Fig. 4) also shows a very normal curve, with no marked extremes. Ground frosts are exceedingly rare.

A series of evaporimeter readings was taken at different levels in the main habitats, and they show very striking differences; the highest evaporation was on the heather slopes, the lowest in the marsh at Garry Loch, which is very sheltered, with a thick carpet of *Sphagnum*. The following readings have



been taken for 1 hour in each case, and have been corrected for the variations in the factors of the evaporimeters used:

Locality	Evaporation in c.c. per hour
Summit	1.02
Garry Loch	0.84
Under boulders (600 ft.)	0.90
Heather slopes	1.32
Beach among boulders	0.96

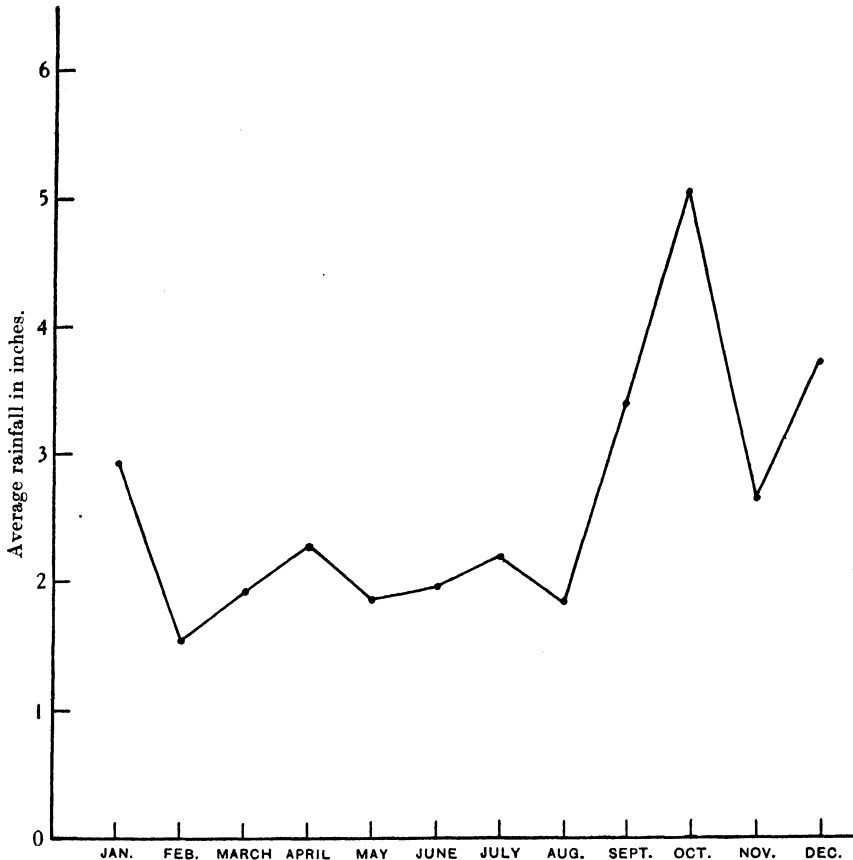


FIG. 3. Ailsa Craig—graph of average rainfall for years 1932-5.

#### GEOLOGICAL AND SOIL FACTORS

Ailsa Craig was formed during the Carboniferous period as the plug to a volcanic vent in the Silurian and Ordovician strata, which no doubt form the floor of the surrounding seas. This plug consists of a fine-grained microgranite, in which the size of the crystalline components varies according to locality. It is characterised by a ground matrix of orthoclase-felspar and quartz, in which are set crystals of a very rare dark blue variety of hornblende, known as

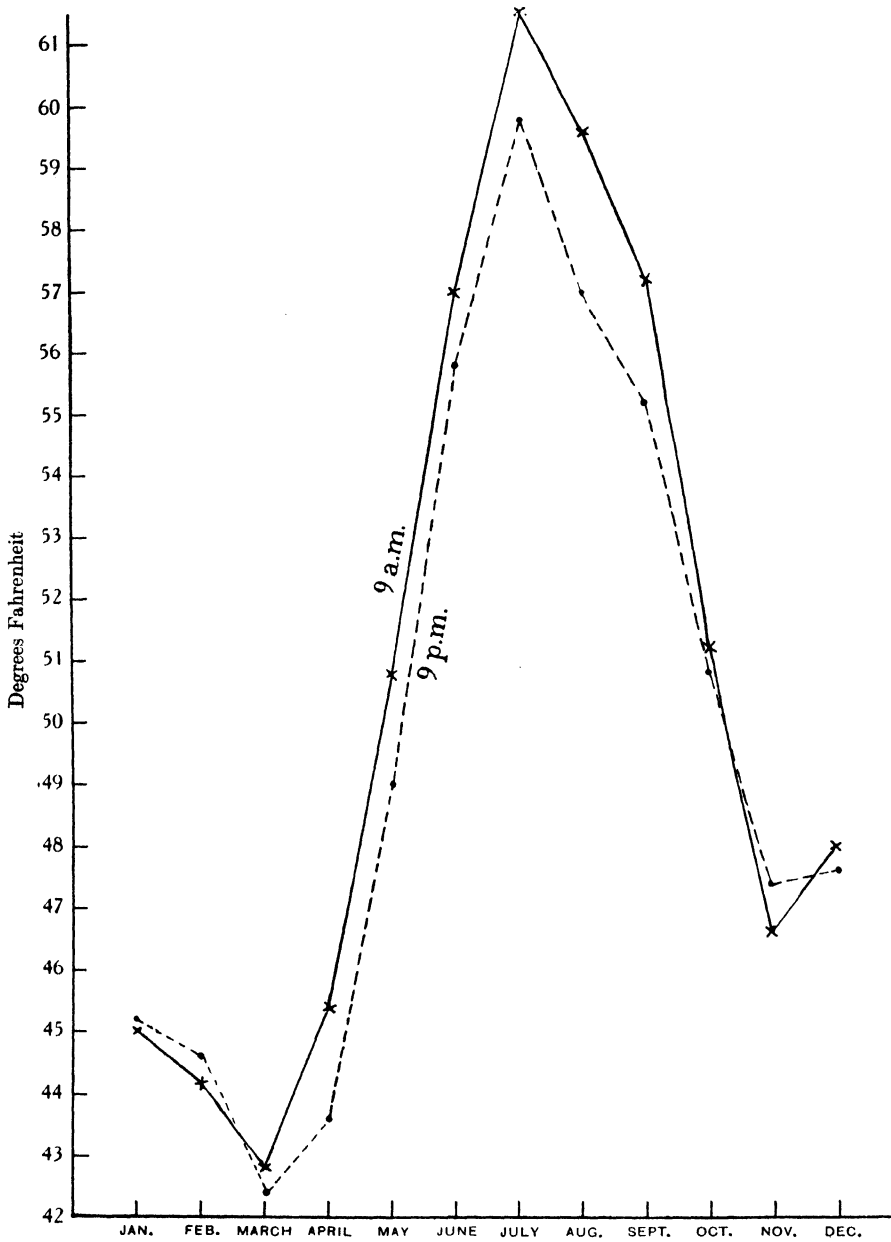


FIG. 4. Graph of air temperatures on Ailsa Craig at 9 a.m. and 9 p.m.; using the average temperatures for every month.

riebeckite (a silicate of sodium and iron with the formula  $\text{Na}_2\text{O} \cdot \text{Fe}_2\text{O}_3 \cdot 4\text{SiO}_2$ ). On the southern and western sides of the rock the granite appears as tall perpendicular columns forming the bird cliffs with their characteristic vegetation.

In addition to the granite there are a number of dolerite or whin dykes, which have appeared as intrusions in the granite probably during the Tertiary Era. This dolerite is more easily weathered than the granite with the result that, where it occurs, rock clefts, caves and small ravines have been formed. Most of the dykes on the south and west sides have an average thickness of 6 ft., but the Swine Cave on the north side has been weathered out from a dyke which is 57 ft. thick.

During the Ice Age the whole of Ailsa was covered in the drift, and at the end of the period a thin layer of detritus was left on the island. This probably formed the first soil of the post-Glacial period. To support the theory of this deposition on the upper slopes of the Craig, I have found a large granite boulder on the ridge north of the Garry Loch at about 850 ft., which I take to be an erratic. The boulder is obviously contorted and, although composed of some form of granite, the texture is totally different from that of the riebeckite-microgranite.

Owing to the steep nature of the slopes and to the action of the rain, the soil is never very deep. It varies from an average of only 6 in. on the heather slopes to 2 ft. in parts of the summit grass association. As will be seen below, the angle of the slope, which determines the thickness of the soil, is one of the main factors influencing the nature of the existing vegetation.

The water supply is abundant and generally distributed over the main slopes; drainage is good, and not too fast except on the heather slopes which are exceedingly steep. The most interesting source of water is the Garry Loch, where there are actually two very small lochs surrounded by a well-drained *Sphagnum* bog. They have been sounded to a depth of 17 ft. without touching the rock. Whether this fissure in the granite penetrates much farther it is at present impossible to say.

The soil on the island is in general acidic. The following list shows the pH value of the soil in each of the important habitats.

*pH values of the soils*

Habitat	pH value
Guano at foot of bird cliffs	6.6-7.0
Rock clefts and caves	6.0
Heather slope	5.7
Bracken slopes (top layer of soil)	5.7
Springs and rills	5.5
Talus slopes	5.2
Summit grassland	5.0
Bracken slopes (bottom layer)	4.5
Under boulders (600 ft.)	4.1

From this list it will be seen that the guano forms an additional factor influencing the soil. It is produced by the enormous bird colony on the south

and south-west sides, and it is only here that it has any marked effect. It occurs on the ledges of the cliffs and at the foot of the latter, but owing to the amount of rain it does not of course accumulate. The modifications which it brings about will be dealt with under special habitats.

#### BIOTIC FACTORS

These factors fall naturally into three categories:

- (1) The effect of the mammals.
- (2) The effect of the sea birds.
- (3) The effect of the land birds.

(1) The rabbits and Soa sheep are responsible for the cropping of the grass and associated plants on the summit grass association, while the goats confine their activities to the lower slopes and eat large quantities of *Scilla nonscripta* and many of the grasses on the talus slopes. They have a strong restricting action on any rare plants which may have succeeded in gaining a foothold. For instance the tree mallow only persists in those parts of the cliffs at the West Trammins which are entirely inaccessible to the goats (Pl. XXII, phot. 11).

(2) The effect of the sea birds by their production of guano will be dealt with more fully below. The sea birds as a whole do not seem to be of importance in the carrying of seed to the island, mainly because their diet is of fish and the majority of them (i.e. the gannets, razorbills and guillemots) scarcely, if ever, alight on the mainland.

(3) The land birds, especially the blackbird and song thrush, probably play an important part in planting seeds on the rock.

#### VEGETATION

It has seemed most natural to describe the vegetation according to the very distinct types of habitat found on the island, as follows:

- (1) *Main slopes*, above 400 ft., at an angle of 20–30°:

- (a) Summit grass association.
- (b) General boulder screes.
- (c) Valleys and ravines, usually wet.
- (d) Bracken belt.

(2) *Heather slopes*, below 400 ft., at an angle between 30 and 50°, hence with increased drainage and thinner soil than the main slopes.

- (3) *Special localised habitats*:

- (a) Rock clefts and caves.
- (b) Bird cliffs.
- (c) Foot of cliffs:
  - (i) with talus slopes;
  - (ii) without talus, but water usually present.

(4) *Marsh and fresh-water habitats:*

(a) Marsh and Garry Loch.

(b) Springs and rills.

(5) *Beach above high-tide*, including the boulder lichen association.

The large-scale vegetation chart (Fig. 1) was drawn in April 1935 on the 25-in. map of the Ordnance Survey, and has been transferred to the 6-in. map (1 : 10,560) for reproduction. Contours are not given on the Ordnance maps, presumably on account of the difficult and rough nature of the slopes.

## (1) MAIN SLOPES

Under this heading I have grouped all those parts of the island above 400 ft. The angle of the slope is between 20 and 30°, except the part between the Castle and the Garry Loch which is much steeper and may have an angle of between 40 and 50°. This area contains a number of different habitats which have been determined almost entirely by the physiographic and edaphic factors. The most important of these are:

(i) The amount of water.

(ii) The presence or absence of boulders.

(iii) The thickness of the soil.

(a) *Summit grass association*

This grassland occurs from the summit down almost as far as Garryloch to the south-east, and to the tops of the cliffs on the north, west, and south-west (Pl. XXI, photos. 5 and 6). It is well exposed to the wind in all parts, and the evaporimeter showed a reading of 1.01 c.c. in 1 hour. The soil is loose and contains a large percentage of organic matter, with the result that the reaction is distinctly acid, showing a *pH* of 5.0. In addition to these a strong biotic factor is involved; for the rabbits, found all over the island, are here living in enormous numbers. Their nibbling keeps the turf very closely cropped, so that the plants grow out sideways and form a dense, compact carpet.

The following plants are found in this association:

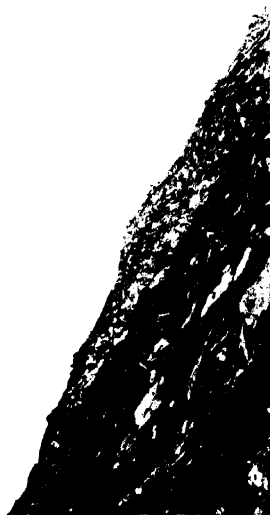
<i>Agrostis canina</i>	a.	<i>Dicranum scoparium</i>	f.
<i>Festuca ovina</i>	a.	<i>Hylocomium squarrosum</i>	f.
<i>Galium saxatile</i>	a.	<i>Hypnum cupressiforme</i> var. <i>ericetorum</i>	f.
<i>Rumex acetosella</i>	f.	<i>Polytrichum juniperinum</i>	f.
<i>Luzula campestris</i>	o.	<i>Mnium hornum</i>	o.
		<i>Cladonia rangiformis</i>	o.
		<i>C. sylvatica</i>	o.

In the rabbit burrows *Lophocolea bidentata* is common and very constant. The turf is interspersed with a large number of well-embedded boulders (Pl. XXI, phot. 6). These are worn and smooth and the effect is quite different from that of the boulders on the general stony screes. In this habitat they support the following species on the upper surfaces:

<i>Parmelia saxatilis</i>	f.	<i>Cladonia pyxidata</i>	o.
<i>Cladonia coccifera</i>	o.	<i>C. uncialis</i>	o.



Phot. 6. General view of summit grass association with embedded rocks.



Phot. 8. Heather slopes at 390 ft. in foreground, with boulder slopes in background.



Phot. 5. Summit grassland near Kennedy's Nags



Phot. 7. Main boulder scree at 600 ft.



*(b) General boulder screes*

These screes form a well-marked habitat commencing about 100 ft. below the summit and descending to the 500-ft. level. They do not form a continuous band, however, but are found as isolated patches. The largest scree is situated 100 ft. below and east of the Garry Loch (Pl. XXI, phot. 7); others are on the sides of Nettleby Howe, Clashwaun and Garryloo. They are formed by the gradual weathering and subsequent dislodging of parts of the cliffs. All the boulders are, of course, angular, and as they have fallen on top of each other there is no intervening soil exposed. They support the following vegetation on their upper surfaces:

<i>Brachythecium rutabulum</i>	f.	<i>Buellia aethalea</i>	a.
<i>Eurhynchium myosuroides</i>	f.	<i>B. saxatilis</i>	a.
<i>Hypnum cupressiforme</i>	f.	<i>Cladonia coccifera</i>	a.
<i>Dicranoweisia cirrata</i>	o.	<i>C. flabelliformis</i>	a.
<i>Grimmia trichophylla</i>	r.	<i>C. pyxidata</i>	a.
		<i>Lecanora coilocarpa</i>	a.
		<i>Parmelia saxatilis</i>	a.

Underneath the boulders conditions are entirely different. The soil is again scarce, but very acid in reaction with a *pH* 4.1. There is also the low evaporimeter reading of 0.90 c.c. in 1 hour. The vegetation is well sheltered and in almost complete shade; it consists of the following species:

<i>Athyrium filix-foemina</i>	f.	<i>Lychnis dioica</i>	o.
<i>Urtica dioica</i>	f.	<i>Pteridium aquilinum</i>	o.

*(c) Valleys and ravines*

A minor habitat found on the main slopes in localised areas, e.g. the valley leading down to Red Gair on the north side. It is very similar to the summit grass association, but is varied to a certain extent by the wetter soil which receives the drainage from the upper slopes. This extra dampness combined with a greater degree of shelter has produced a characteristic moss association on the slopes of each valley.

The following species are found:

<i>Agrostis alba</i>	d.	<i>Mnium hornum</i>	f.
<i>Poa annua</i>	a.	<i>Catharina undulata</i>	o.
<i>Plagiothecium undulatum</i>	a.	<i>Plagiothecium denticulatum</i>	o.

There are a few rocks which support the following mosses and lichens:

<i>Eurhynchium myosuroides</i>	a.	<i>Cladonia coccifera</i>	f.
<i>Hypnum cupressiforme</i>	a.	<i>C. subsquamosa</i>	f.

*(d) Bracken slopes*

This bracken belt occurs extensively on the eastern slopes of the rock, between the 400 and 500 ft. levels, that is, above the heather slopes. In these parts the angle of the slope is never very great and there is, in consequence, a much thicker covering of soil. The existence of this community here may be attributed to the above factor and to shelter from the more violent winds.



The dominant plant is *Pteridium aquilinum*, although *Scilla nonscripta* is more abundant in individuals (Pl. XXIII, phot. 13). It will also be seen from the quadrat chart that the bracken plants are scattered very evenly throughout the square metre, whereas those of *Scilla nonscripta* are found aggregated in small groups of about 6–12 plants in each. This arrangement probably plays an important part in allowing the hyacinths a greater amount of light while the bracken is still half-grown.

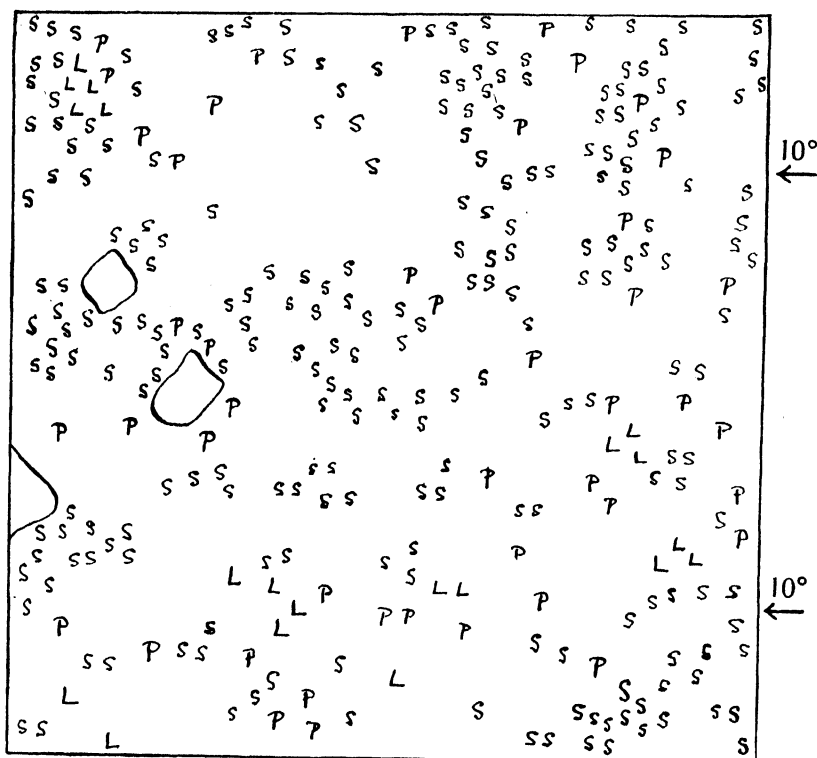


FIG. 5. Quadrat of 1 sq. m. of bracken slope. Altitude 500 ft.  
S = *Scilla nonscripta*, P = *Pteridium aquilinum*, L = *Lychnis dioica*.

The profile section taken in spring (Fig. 6) shows that the three species of flowering plants live under very different conditions. The hyacinth has its roots and bulb at 20–22 cm., surrounded by a soil with pH 4.5, and it sends up leaves and flowers in the spring. The bracken grows from a rhizome which is 10 cm. below the surface, is surrounded by a soil with a pH of 5.7, and it sends up its fronds in the late summer and sheds its spores in the early autumn months. The campion roots are shallower still.

The following is the full list of species from this habitat:

<i>Pteridium aquilinum</i>	d.	<i>Bryum capillare</i>	o.
<i>Scilla nonscripta</i>	a.	<i>Hypnum cupressiforme</i> var. minus	o.
<i>Lychnis dioica</i>	f.		

The variety *minus* of *H. cupressiforme* is a new county record for Ayrshire, and this is the only part of the island in which it has been found.

## (2) HEATHER SLOPES

Like the bracken slopes this habitat only occurs on the east and north-east sides, where it extends from the 400-ft. level down to 20 ft. above sea-level in most places. The main part is situated just below the Castle Comb. The angle of slope is usually between 30 and 50°, although in parts it may be as much as 75°. Where these very steep parts occur, the vegetation is seen as

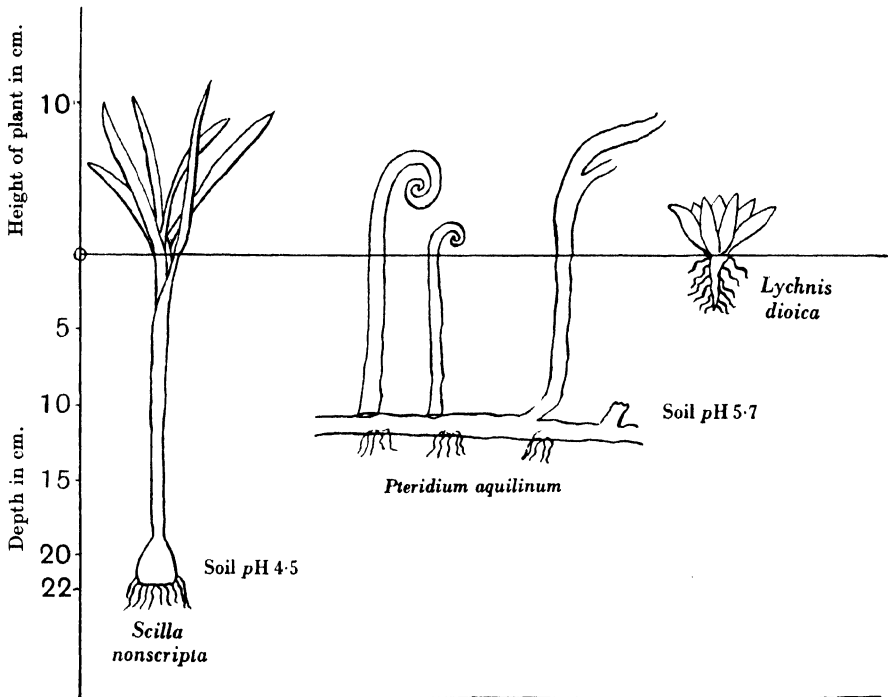


FIG. 6. Profile section of bracken slope.

elongated, narrow, more or less horizontal ridges about  $3 \times \frac{1}{2}$  m., supported below by outcrops of granite *in situ* (Pl. XXI, phot. 8).

Owing to the angle of the slope the thickness of the soil is very much reduced and the pH is 5.7, that is, acid but not so pronounced as in many other parts of the island. The quadrat (Fig. 7) shows that the dominant plant is *Erica cinerea*, and that *Scilla nonscripta* occurs here again although only occasionally. It will also be seen that the flowering plants grow in well-marked usually curving ridges, with the intervening soil either bare or covered with scattered lichens or mosses. It is noteworthy that *Calluna* is only occasional and does not occur in the quadrat figured.

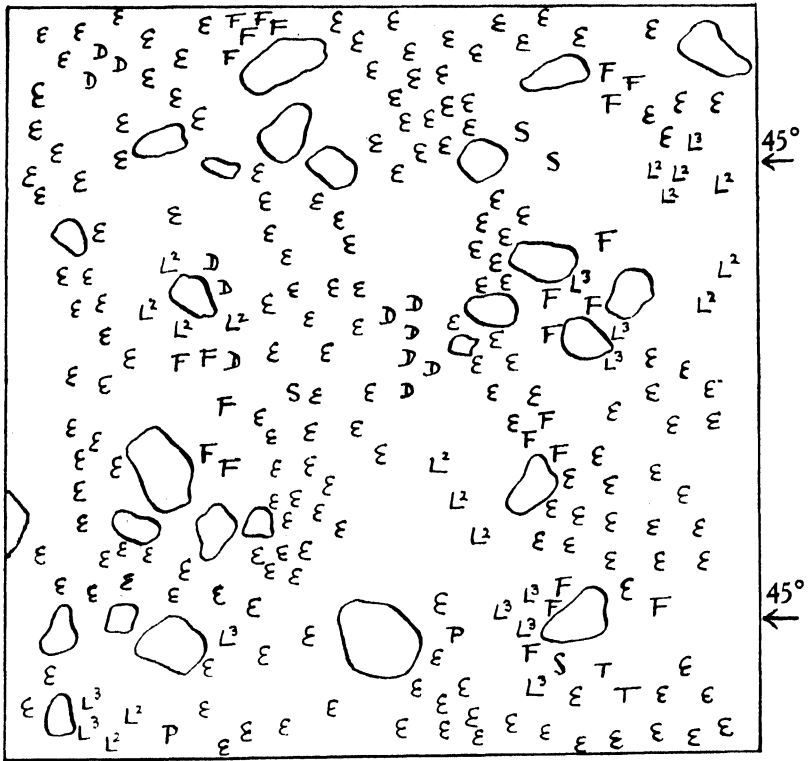


FIG. 7. Quadrat of 1 sq. m. of heather slope. Altitude 390 ft. *E*=*Erica cinerea*, *F*=*Festuca ovina*, *S*=*Scilla nonscripta*, *T*=*Teucrium scorodonia*, *P*=*Polytrichum juniperinum*, *D*=*Dicranum scoparium*, *L*<sup>2</sup>=*Cladonia uncialis*, *L*<sup>3</sup>=*C. sylvatica*.

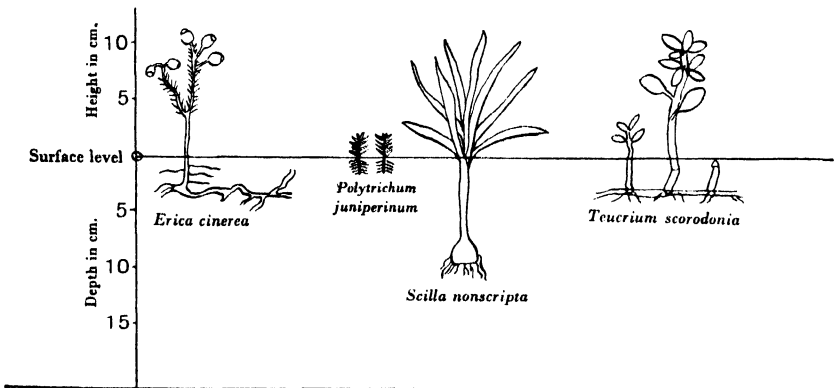


FIG. 8. Heather slope. Profile section to show the relative depths of the root-systems and heights of aerial parts in the representative plants.

A profile section (Fig. 8) shows that *Erica cinerea* has its root system at 4 cm., the same level as *Teucrium scorodonia* which is only frequent in this habitat. *Scilla nonscripta* cannot penetrate so far as it does in the bracken slopes, and I found the bulb at 10 cm. below the surface. The top centimetre of the soil was occupied by the roots of *Polytrichum juniperinum* and *Dicranum scoparium*.

Flora of heather slope:

<i>Erica cinerea</i>	d.	<i>Campylopus pyriformis</i>	f.
<i>Teucrium scorodonia</i>	f.	<i>Dicranum scoparium</i>	f.
<i>Festuca ovina</i>	f.	<i>Polytrichum juniperinum</i>	f.
<i>Calluna vulgaris</i>	o.	<i>Hypnum cupressiforme</i>	o.
<i>Scilla nonscripta</i>	o.		
<i>Potentilla erecta</i>	o.	<i>Lophozia ventricosa</i>	o.
<i>Viola canina</i>	r.		
<i>Fragaria vesca</i>	r.	<i>Cladonia pyxidata</i>	a.
		<i>C. sylvatica</i>	a.
		<i>C. uncialis</i>	a.
		<i>Parmelia saxatilis</i>	f.
		<i>Sphaerophoron coralloides</i>	o.

It is surprising to find such a large number of species growing in this habitat, for the conditions do not seem very favourable. In addition to the thin soil, the situation is very exposed, and it showed the highest evaporimeter reading in the island, 1.32 c.c. in 1 hour. But it will be noticed that many of the plants have xeromorphic features. Among the angiosperms, apart from *Erica cinerea* which is highly xeromorphic, *Teucrium scorodonia* has a thick cuticle which is hairy and *Festuca* a very narrow leaf with reduced lamina. Among the mosses, *Polytrichum juniperinum* and *Dicranum scoparium* have leaves which can be adpressed to the stem. The lichens can, of course, withstand almost any extreme of desiccation.

### (3) SPECIAL LOCALISED HABITATS

#### (a) Rock clefts and caves

Rock clefts occur at the foot of the cliffs all round the island and in three places give rise to well-formed caves, mostly where dolerite dykes, more quickly weathered, traverse the granite. These clefts are very well sheltered from the wind and one of the factors determining the vegetation is always the small trickle of water which drips from the sides and the roof. As the sides are nearly always perpendicular the amount of soil retained in the cracks is limited, and very little anchorage is supplied. The soil on the floor of the cave or cleft is sodden and compact, and has a pH of 6.0.

The sides yielded the following flora:

<i>Asplenium marinum</i>	d.	<i>Marchantia hemisphaerica</i>	a.
<i>Cotyledon umbilicus</i>	a.	<i>Mnium hornum</i>	f.
		<i>Porotrichum alopecurum</i>	f.

The growth of the sea spleenwort and navelwort is here very luxuriant, the fronds of the former reaching a length of 18 in., while the latter is usually about 2 ft. high when in flower.

In the inner parts of the clefts the floor is covered with goat droppings,

pieces of dried stems, and a few bones, and it supports no vegetation. In the outer parts, *Cochlearia officinalis* is very abundant, both as seedlings and as mature plants. Other species found are:

<i>Agrostis canina</i>	a.	<i>Camptothecium sericeum</i>	f.
<i>Viola canina</i>	f.	<i>Hypnum cupressiforme</i>	f.

(b) *Bird cliffs*

The cliffs extend all round the west, south, and part of the north coasts of the island, but only in certain areas are they inhabited by the sea birds. All these cliffs may be treated together, because there is no significant difference between their floras. All the plants living in this habitat, except the lichens, must grow either in rock cracks or in soil on the ledges (Pl. XXII, photos. 9 and 10; Pl. XXIII, photos. 14 and 15). There is very little soil in this situation, and it is variable in composition, with a *pH* between 6.0 and 6.5. The following plants are found growing on the cliff ledges:

<i>Agrostis tenuis</i>	<i>Raphanus maritimus</i>
<i>Cochlearia officinalis</i>	<i>Rosa canina</i>
<i>Cotyledon umbilicus</i>	<i>Sambucus nigra</i>
<i>Festuca ovina</i>	<i>Scabiosa succisa</i>
<i>Fumaria capreolata</i>	<i>Silene maritima</i>
<i>Glyceria maritima</i>	<i>Spergularia rupicola</i>
<i>Jasione montana</i>	<i>S. salina</i>
<i>Lavatera arborea</i>	

The specimens of *Sambucus nigra* never grow very large because of the limited supply of soil, but they seem to seed freely; this is a plant whose seed is easily sown by birds, especially the blackbird. The tree mallow (*Lavatera arborea*) is only found on ledges at the West Trammins and it is no doubt restricted to these inaccessible spots on account of the goats (Pl. XXIII, phot. 15). This is said to be the only place where it is indigenous in the Clyde Area.

The two woody climbers, ivy and honeysuckle, are found commonly rooted either on the ledges or in large cracks, their stems straggling over the surface of the rock. There are also a few plants which grow in the small cracks and sometimes even on the rock surface:

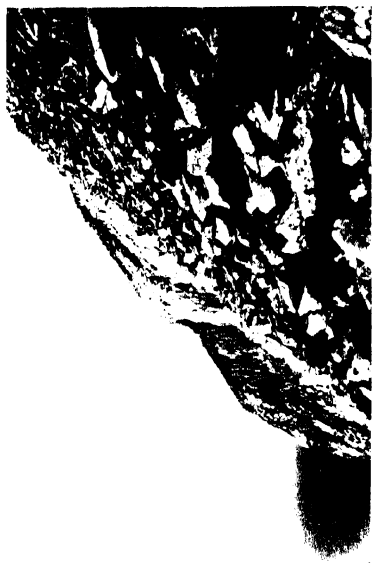
<i>Plantago coronopus</i>	<i>Camptothecium sericeum</i>
<i>Sedum anglicum</i>	

Lichens are omitted because the species found on the rock faces are in general the same as those on the boulders above high-tide (see under (5) Beach above high tide).

This habitat has an important effect on the flora of the island because nearly all the plants must have been carried to the Craig by birds; and as this is the usual resting place for the latter, it is probably also the first site for many of the colonists.

(c) *Foot of cliffs*

Very distinct habitats have been formed at the foot of the cliffs on the north, south and west coasts. In the two latter areas talus slopes have been formed at the bottom of the cliffs, while on the north side many of the cliffs come down directly to the shore.



Phot. 10. Gannets on Balraer from just south. Vegetation showing *Silene* and *Lychnis*.



Phot. 12. Beach above high-tide, north of lighthouse.



Phot. 9. Kittiwakes in the Slunk, also showing cliff vegetation.



Phot. 11. Talus slopes below Main Craigs, looking S.E.; also showing Little Ailsa in centre.



(i) *With talus slopes at an angle between 30 and 40°.*

The talus is composed of detritus washed or blown down from the slopes above the cliffs, and of granite blocks which have been eroded from the cliffs themselves. When these slopes occur in parts uninhabited by the sea birds, the soil is a loose, slightly peaty humus of pH 5.2. It is always kept moist by the drainage of water from the cliffs. The surface is strewn with granite blocks

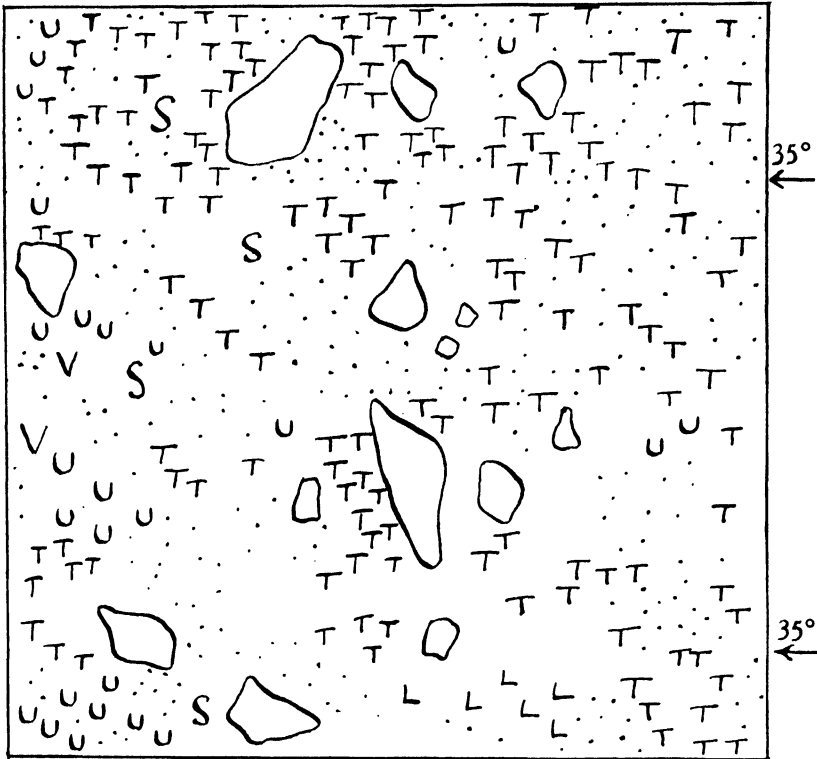


FIG. 9. Quadrat of 1 sq. m. of partly stabilised talus slope. *T* = *Teucrium scorodonia*, *U* = *Urtica dioica*, *S* = *Senecio jacobaea*, *L* = *Lychnis dioica*, *V* = *Viola canina*, • = *Holcus mollis*.

and chips, the former having an average area of 1 sq. m. These acid places support the following flora:

<i>Teucrium scorodonia</i>	d.	<i>Galium saxatile</i>	f.
<i>Urtica dioica</i>	v.a.	<i>Pteridium aquilinum</i>	f.
<i>Cardamine hirsuta</i>	v.a.	<i>Senecio jacobaea</i>	f.
<i>Lychnis dioica</i>	a.	<i>Lycopsis arvensis</i>	o.
<i>Holcus mollis</i>	a.	<i>Urtica urens</i>	o.
<i>Poa annua</i>	a.	<i>Erodium cicutarium</i>	r.
<i>Carduus crispus</i>	f.	<i>Sambucus nigra</i>	r.
<i>Cotyledon umbilicus</i>	f.		

The quadrat represented in Fig. 9 shows that the vegetation is fairly compact, and this is in contrast to that of the following variety. For when these talus slopes occur under the bird cliffs, the conditions are entirely different.



The soil is not so uniform in composition and contains a large amount of refuse from the nests, especially bones, as well as guano. On those slopes where guano is present the pH of the soil is 7.0, and that is the nearest approach to an alkaline soil on the island. The vegetation in these cases is very poor, and only the following species occur:

<i>Lychnis dioica</i>	d.	<i>Urtica dioica</i>	o.
<i>Poa annua</i>	f.		

I have come to the conclusion that this contrast between the two varieties of talus slopes is not due entirely to the pH of the soil, but that the increase of debris and other rough material on the bird talus slopes plays an important part. This means that in this latter variety the talus slopes are even less stabilised than those which are not affected by the sea-fowl. Any stabilisation which may take place during one summer is nullified by the falls of rock and the heavy drainage from above in the succeeding winter. This results in the restriction of the vegetation to such annuals or biennials as *Poa annua* or *Lychnis dioica*, and to only a few perennials which are ubiquitous, e.g. *Urtica dioica*.

(ii) *Without talus*, but water usually present.

In this habitat no detritus is accumulated and the foot of the cliffs descends directly to the beach above high tide. A spring is usually present and the species are nearly all moisture-loving bryophytes and lichens. This type of habitat occurs at the foot of the cliffs on the north coast only, and is very well shown along the part known as the Loups. The following species are found:

<i>Holcus mollis</i>	a.	<i>Frullania germana</i>	f.
<i>Bryum alpinum</i>	a.	<i>Pellia epiphylla</i>	f.
<i>Porotrichum alopecurum</i>	a.	<i>Scapania undulata</i>	f.
<i>Eurhynchium myosuroides</i>	f.	<i>Peltigera canina</i>	a.
<i>Sphagnum cuspidatum</i>	r.	<i>P. horizontalis</i>	a.

#### (4) MARSH AND FRESH-WATER HABITATS

The only true marsh locality is the Garry Loch, but there are a number of springs which flow down the slopes in all parts of the island. The latter support a vegetation which is typically aquatic, although differing from that of the true marsh.

##### (a) *Marsh and Garry Loch*

The marsh in this locality would be more accurately described as a *Sphagnum* bog with two small lochs in the middle. The bog is absolutely level, but the drainage is good, by means of an outlet at the north end (Pl. XXIII, phot. 16). The situation is one of the most sheltered on the island; the evaporimeter showed the very low reading of 0.84 c.c. in 1 hour. The conditions are therefore ideal for the growth of *Sphagnum* plants. The following flora list has been compiled:



Phot. 13. Quadrat on bracken slope. Leaves of *Scilla* may be seen in centre.



Phot. 14. Bird cliffs at Ashyadoo, showing typical vegetation.



Phot. 15. Tree mallow (*Lavatera arborea*) growing on the West Trammins.



Phot. 16. Garry Loch, looking north from Garraloo, showing *Sphagnum* bog and the outlet at the north end.



<i>Sphagnum cuspidatum</i>	d.	<i>Caltha palustris</i>	f.
<i>S. cymbifolium</i>	d.	<i>Galium saxatile</i>	r.
<i>S. fimbriatum</i>	d.		
<i>Polytrichum strictum</i>	a.		
<i>Aulacomnium palustre</i>	a.		
<i>Hylacomium squarrosum</i>	r.		

The *Caltha palustris* was only present round the edges and near the outlet, and the *Galium saxatile* was an obvious intruder from the summit grass association of the slopes above.

(b) *Springs and rills*

The springs all flow down very steep parts of the rock, and as they cannot cut into the subsoil to any depth their effect is mainly on the surface where they form rills. There is a good example below the Castle Well but the best rill is below the Horse Well, which is about 40 ft. above sea-level and furnishes the supply of water to one of the tenant's houses. The flora is very characteristic:

<i>Montia fontana</i>	d.	<i>Polytrichum commune</i>	f.
<i>Philonotis fontana</i>	a.	<i>Lophozia ventricosa</i>	f.
<i>P. caespitosa</i>	f.		

These plants are all either bryophytes or muscoid in their external appearance. The stems of *Polytrichum commune* in this habitat are short, and the whole plant very stunted.

(5) BEACH ABOVE HIGH TIDE

The vegetation of this habitat is essentially rupestral. The rock is either loose as large sea-worn boulders or *in situ* as a few small ridges of rock running out from the main cliffs. The photograph (Pl. XXII, phot. 12) shows the general appearance of the beach including the marine intertidal zone whose upper limit is marked by the dark band of *Pelvetia canaliculata*. A pathway is seen above the beach and above the path the base of the heather slopes.

The evaporationimeter reading for this area was low, 0.96 c.c. in 1 hour, almost the same as the reading taken under boulders at 600 ft. There is no soil except in the hollows in the rock, where a very thin layer is sometimes present. In these places, where there is also a certain amount of moisture, the following species occur:

<i>Armeria maritima</i>	a.	<i>Senecio jacobaea</i>	r.
<i>Cochlearia officinalis</i>	a.	<i>Bryum alpinum</i>	v.r.

On the boulders, however, conditions are quite different, as very little moisture can be retained, and there is only anchorage for mosses and lichens. This results in a true lichen community, with only one moss, *Rhacomitrium lanuginosum*, occasionally present. The following lichens occur:

<i>Buellia aethalea</i>	<i>Physcia fusca</i>
<i>B. colludens</i>	<i>Ramalina Curnowii</i>
<i>Lecanora</i> sp.	<i>R. scopulorum</i>
<i>Parmelia parietina</i>	<i>Rhizocarpon confervoides</i>
<i>P. saxatilis</i>	<i>R. geographicum</i>
<i>Pertusaria</i> sp.	

## SUMMARY AND SUCCESSIONAL SCHEME

Climatic, physiographic and edaphic conditions on Ailsa Craig have all had a very marked determining action on the vegetation and have combined to limit the flora of the island as a whole. The most important factor is the steep slope, which has influenced other factors, especially the edaphic conditions.

The major divisions of vegetation on the island are the bird cliffs and the main slopes. Owing to the various types of bird-cliff vegetation found, it is impossible to say exactly what successional changes have been and are taking place. But on the main slopes a more definite succession can be observed, for there the summit grass association forms the climax type of vegetation. It has been possible to distinguish two well-defined seres (A and B) leading to this climax type, and a third sere (C) leading to another climax, the Heather Slopes.

## A. BOULDER SCREE XEROSERE

(1) In the early stages the surfaces of the boulders are populated by lichens, both crustaceous and foliose, and by a few mosses. The soil between and below the boulders supports a few Angiosperms and *Athyrium filix-foemina*.

(2) Colonisation of the moss tussocks by small grasses and Dicotyledons, e.g. *Galium saxatile*. The next seral stages are not so clear but it is probable that the spaces between the boulders become filled up with detritus which supports an increasing population of grasses and ground mosses. When equilibrium is reached the turf becomes a closed community with interspaced boulders as in the described summit grass association.

## B. RAVINE HYDROSERE

The springs and rills are omitted as they are too localised in occurrence to have any effect on the vegetation in general. But the ravines and valleys occurring on the upper slopes are usually moist and support the damp moss vegetation described above under the section on Valleys and Ravines. This sere has the following stages:

(1) The soil of the sides of the ravines is washed bare, and populated by mosses—*Mnium hornum* and *Catharinea undulata*—forming an open community. Simultaneously there are a few boulders lying in these valleys which follow a succession similar to that on the boulder scree, except that there are more moisture-loving species, e.g. *Hypnum cupressiforme* and *Eurhynchium myosuroides*.

(2) The mosses on bare ground are followed by grasses together with their usual complement of turf-forming mosses, e.g. *Hylocomium squarrosum*. Gradually the grasses spread out sideways to form a closed community and the boulders become half-embedded. In this way the whole sere ends in the summit climax grass association.

## C. HEATHER SLOPE XEROSERE

The heather slopes form a physiographic-edaphic climax dependent on the angle of slope and the consequent drainage.

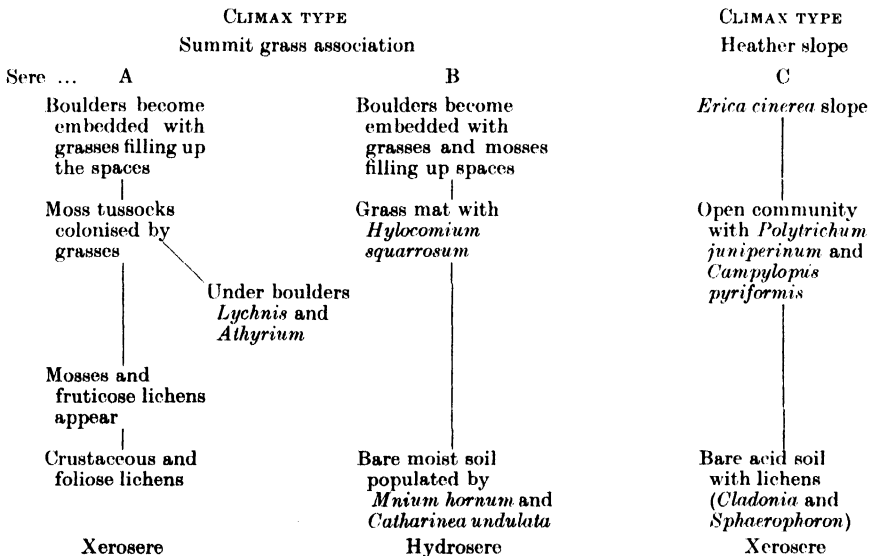
(1) Bare acid soil becomes covered with patches of lichens—*Cladonia* and *Sphaerophoron*.

(2) This may be followed almost immediately by a few mosses—*Polytrichum juniperinum* and *Campylopus pyriformis*, thus forming an open community of moss and lichen.

(3) This stage probably coincides with the colonisation of the *Erica cinerea* and a few other plants, especially along the small ridges mentioned above under heather slope. Although many other plants come in, including grasses, they are unable to replace the *Erica*, on account of the unfavourable conditions.

It seems therefore that, except for these successions taking place in the main and heather slopes, there are very few seral changes going on in the island. The vegetation shows a mixture of oceanic and mainland types on the west cliffs and general slopes respectively. Biotic factors must have been involved in introducing most of the plants, and the summit grass association is clearly influenced by the biotic factor of rabbits and sheep, but it is the physiographic factors, and the edaphic factors consequent on them, which determine whether the new arrivals shall stay and whether they will have any effect in modifying the existing vegetation.

## Successional scheme for general slopes



## LIST OF FLORA

The first list of plants was made by Prof. Balfour and a party of students in 1844. In 1922 W. B. Gourlay and G. M. VEVERS added quite a number of new plants. J. R. Lee (1933) keeps the Ailsa records separate, and his list has been compiled from Balfour's together with that of the Andersonian Naturalists' Club. A number of new records have now been added to these lists, especially among the cryptogams, where three of the fresh records for bryophytes are new to the county of Ayrshire (V.C. 75). The following list is compiled from all these sources:

*Angiosperms*

Agrostis alba	Fumaria capreolata	Ranunculus repens
A. canina	Galium aparine	Raphanus maritimus
A. tenuis	G. saxatile	Rosa canina
Aira praecox	Geranium molle	Rubus fruticosus
Alchemilla arvensis	Glyceria maritima	Rumex acetosa
Angelica sylvestris	Hedera helix	R. acetosella
Anthoxanthum odoratum	Hieracium murorum	R. crispus
Arabis hirsuta	Holcus lanatus	R. obtusifolius
Arctium minus	H. mollis	Sagina maritima
Arenaria peploides	Hydrocotyle vulgaris	S. procumbens
Armeria maritima	Hypochoeris radicata	Sambucus nigra
Arrhenatherum elatius	Jasione montana	Saxifraga hypnoides
Artemisia vulgaris	Juncus bulbosus	Scabiosa succisa
Atriplex glabriuscula	J. squarrosus	Scilla nonscripta
A. littoralis	Lavatera arborea	Sedum anglicum
A. patula	Leontodon autumnalis	Senecio jacobaea
Bellis perennis	Linaria cymbalaria	S. vulgaris
Brassica monensis	Lonicera periclymenum	Scirpus setaceus
Calluna vulgaris	Lotus corniculatus	Silene maritima
Caltha palustris	Luzula campestris	Sisymbrium thalianum
Capsella bursa-pastoris	L. pilosa	Sonchus oleraceus
Cardamine hirsuta	L. sylvatica	Spergularia marginata
C. pratensis	Lychnis dioica	S. rupicola
Carduus crispus	Lycopsis arvensis	S. salina
C. pycnocephalus	Matricaria inodora	Stellaria media
Carlina vulgaris	Montia fontana	Taraxacum vulgare
Cerastium vulgatum	Myosotis arvensis	Teucrium scorodonia
Chenopodium album	M. collina	Thymus serpyllum
Cirsium lanceolatum	M. versicolor	Trifolium dubium
Cochlearia officinalis	Plantago coronopus	T. repens
Corydalis claviculata	P. lanceolata	Urtica dioica
Cotyledon umbilicus	P. major	U. urens
Crepis capillaris	P. maritima	Vaccinium myrtillus
Deschampsia flexuosa	Poa annua	Veronica agrestis
Draba verna	Polygala vulgaris	V. chamaedrys
Epilobium montanum	Polygonum aviculare	V. officinalis
E. palustre	Populus tremula	V. serpyllifolia
Erica cinerea	Potentilla erecta	Vicia lathyroides
Erodium cicutarium	P. reptans	V. sativa
Euphrasia officinalis	Prunella vulgaris	Viola canina
Festuca ovina	Ranunculus bulbosus	Zostera marina
Fragaria vesca	R. flammula	

*Ferns*

Asplenium adiantum-nigrum	Athyrium filix-foemina	Polypodium vulgare
A. marinum	Dryopteris dilatata	Pteridium aquilinum
A. ruta-muraria	D. filix-mas	Scolopendrium vulgare

*Mosses*

Antitrichia curtipendula  
 Aulacomnium palustre  
 Brachythecium rutabulum  
 Bryum alpinum  
 B. argenteum  
 B. atropurpureum  
 B. capillare  
 Campylopus sericeum  
 Campylopus pyriformis  
 Catharina undulata  
 Ceratodon purpureus  
 Dicranoweisia cirrata  
 Dicranum scoparium  
 Eurhynchium myosuroides

Eurhynchium myurum  
 E. praelongum  
 Grimmia trichophylla  
 Hylocomium squarrosum  
 H. triquetrum  
 Hypnum cupressiforme  
     var. ericetorum  
     var. minus  
     var. resupinatum  
 H. fluitans  
 H. stramineum  
 Mnium hornum  
 M. undulatum  
 Philonotis caespitosa

Philonotis fontana  
 Plagiothecium denticulatum  
 P. undulatum  
 Polytrichum commune  
 P. juniperinum  
 P. strictum  
 Porotrichum alopecurum  
 Pterogonium gracile  
 Rhacomitrium lanuginosum  
 Sphagnum fimbriatum  
 S. cuspidatum  
 S. cymbifolium  
 Tortula fallax  
 T. muralis

*Hepatics*

Chiloscyphus polyanthus  
 Conocephalum conicum  
 Frullania dilatata  
 F. germana

Frullania tamarisci  
 Lophocolea bidentata  
 Lophozia ventricosa

Marchantia hemisphaerica  
 Peltia epiphylla  
 Scapania undulata

*Lichens*

Buellia athalea  
 B. colludens  
 B. saxatilis  
 Candelaria concolor  
 Cladonia bellidiflora  
 C. coccifera  
 C. flabelliformis  
 C. furcata  
 C. macilenta  
 C. pyxidata  
 C. rangiferina  
 C. rangiformis

Cladonia subsquamosa  
 C. sylvatica  
 C. uncialis  
 Collema cristatum  
 Lecanora coilocarpa  
 L. parella  
 Lobaria pulmonaria  
 L. scrobiculata  
 Parmelia squila  
 P. caperata  
 P. furcata  
 P. olivacea

Parmelia saxatilis  
 Peltigera canina  
 P. horizontalis  
 Physcia fusca  
 Ramalina curnowii  
 R. scopulorum  
 Rhizocarpon confervoides  
 R. geographicum  
 Sphaerophorus compressus  
 S. coralloides  
 Usnea plicata  
 Xanthoria parietina

## REFERENCES

- Balfour, J. H. *Phytologist*, 2, 257, 1845.  
 Gourlay, W. B. and Ververs, G. M. Unpublished list of flora, 1922.  
 Lee, J. R. *Flora of the Clyde Area*. Glasgow, 1933.



# THE BRYOPHYTES AND LICHENS OF BRITISH WOODS. PART II, OTHER WOODLAND TYPES

By W. WATSON

## INTRODUCTION

THE beech woods and some of their serals have been dealt with in Part I,<sup>1</sup> and the oak, ash, birch, alder and coniferous woods will be dealt with in this part. The bryophytic and lichen constituents of the Somerset woods have been well worked, and therefore give a solid foundation on which can be laid the material gleaned from work in other parts of our islands. In some Somerset woods natural conditions prevail, but in many others there is much interference by man. This interference does not seem to have affected the bryophytes and lichens to the same extent as it has the higher plants, but some woods have had to be neglected on this account, whilst others have needed careful correlation with more natural woods in other parts of the country. Similar care has had to be taken with the various woods investigated in other counties. The most natural woods are those on the west of our island and in the Highlands of Scotland, but even in some of these one finds evidence of man's interference not only by deforestation and cultivation but also in other ways. From a bryophytic point of view perhaps the most serious of these ways is the diversion and collection of water for the supply of large towns, whilst the lichens have been more seriously affected by the contamination of the air.

Some difficulty has been experienced in regard to the nomenclature of the oak woods. Most *Quercus robur* woods occur on more or less clayey soils which are more retentive of moisture than the shallower lighter soils on which *Q. sessiliflora* woods usually occur. On this account the former have been sometimes styled "damp oak woods" and the latter "dry oak woods". A pedestrian passing through these two kinds of wood after a wet day would think about the state of his boots and probably agree with this classification. However, the *Q. sessiliflora* woods of the west are usually well irrigated, the amount of water precipitated and passing through them is usually considerably greater than in the *Q. robur* woods and it is better to avoid these ambiguous names. In an earlier paper on the Bryophytes of the Woodlands of Somerset (Watson, 1909) three types of woodland were distinguished: oak, oak-hazel and ash. The bryophytes listed for the "oak" are characteristic of the *Q. sessiliflora* woods. The term "oak-hazel" was used in a local sense for the woods "at low elevations on the Triassic and Jurassic marls and clays" in which *Q. robur* and *Corylus avellana* are "the dominant woody plants while ash standards are of infrequent occurrence". The bryophytes listed for these are

<sup>1</sup> Part I appeared in this JOURNAL, 24, pp. 139-61.

characteristic of *Quercus robur* woods. In some of the "transition" woods, ash became more frequent and the plants found in these are listed in the present article under ash-oak woods. These ash-oak woods are quite distinct from the ashwoods of the Mendips and, though the soil on which they occur is usually somewhat stiff, may extend over Triassic sandstone or Greensand.

#### WOODLANDS INVESTIGATED

Many woods in various parts of our country have been more or less investigated in regard to their bryophytes and lichens. The following list, arranged in vice-comital order, gives a general idea of the positions of these woods and by whom they were examined. In some cases the investigation was made during a meeting of a Society such as the British Ecological Society (B.E.S.), the British Bryological Society (B.B.S.) or the British Mycological Society (B.M.S.), and indications of this are given in the list. Some information as to the results can in some cases be obtained from the Reports of these Societies. Those of the B.M.S. appeared in the *Trans. Brit. Mycol. Soc.* at a later date and give useful information about the fungi, which are otherwise little considered in this paper. Most of the woods have been personally examined, even most of those with a reference to an author attached. The names of particular woods are not usually given unless there is some later reference to them in the text.

#### *England and Wales*

*Cornwall*: Trevaylor, Mount Edgecumbe.

*Devon*: Borders of Dartmoor (B.M.S. 1935) and Exmoor (B.B.S. 1932), Wistmans Wood, Black Tor Copse, Lydford Gorge, Holne Chase, Cornwood, Bovey Valley, Upper Yealm Valley.

*Somerset*: Natural woods of most kinds (Watson, 1909, etc.) except beech woods are present. Clusters of beeches are sometimes present in other woods and such a cluster in Cleeve Combe was described as a beech wood in *Trans. Brit. Mycol. Soc.* 1924. Horner Wood, Holford Combe, Shapwick, Chard Common, Longleat.

*Wiltshire*: Stourton woods, Bradley, Savernake.

*Dorset*: Morden, Studland, Purbeck Hills (B.B.S. 1930).

*Hampshire*: New Forest, Ditcham Park (Adamson, 1921), Knightswood, Matley.

*Sussex*: South Downs (Watt, 1923-4), Henley, East Dean.

*Surrey*: Haslemere (B.M.S. 1932), Hindhead.

*Essex*: Epping (Paulson, 1914, 1918).

*Hertfordshire* (Salisbury, 1916, 1918).

*Middlesex*: General (Richards, 1928), Ickenham. The woodland is poor for bryophytes and lichens. As in so many other woods around London, the flora has been much affected by smoke.

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*Buckinghamshire*: Chilterns (Watt, 1934), Burnham Beeches.

*Norfolk*: Plumstead, Stratton Strawless and other woods near Norwich (B.M.S. 1934).

*Gloucestershire*: Wye Gorge (Armitage, 1914), Forest of Dean (Knight, 1914), Cotswolds, May Hill, Symonds Yat, Blaise Castle (B.M.S. 1923).

*Herefordshire*: Ross district (B.B.S. 1925).

*Worcestershire*: Malvern (Salisbury and Tansley, 1921), Wyre (Salisbury, 1925).

*Staffordshire*: Cannock Chase. An almost pure birchwood occurs near Rugeley.

*Brecon*: Blaen Hepste (B.B.S. 1927).

*Cardigan*: Devil's Bridge, Aberystwyth (B.E.S. 1925).

*Merioneth*: Dolgelly (B.B.S. 1922), Tyn-y-Groes, Artro Valley, Nantcol, Cwm Bychan (B.B.S. 1931).

*Carnarvon*: Cwm-y-Glo, Llanberis, Aberglaslyn, Maentwrog (B.B.S. 1924).

*Denbigh*: Nant-y-Ffrith.

*Flint*: Leet.

*Leicestershire*: (Horwood, 1909).

*Nottinghamshire*: (Hopkinson, 1927).

*Derbyshire*: Edale, Kinder, Castleton, Monsal Dale to Buxton.

*Cheshire*: Alderley, Lindow, Staley Brushes, Crowden.

*Yorkshire*: Wharfedale, Bolton Woods, Swaledale, Ribblesdale, Forge Valley and Pickering (B.E.S. 1927), Ingleton (B.B.S. 1934), Pennines.

*Westmoreland and Cumberland*: Keskadale and Birkrigg (Leach, 1925), Lake District (B.B.S. 1933), Esthwaite, Tilburthwaite.

*Isle of Man*: Tholt-y-Wills, Sulby and Groudle Glens (Watson, 1933).

### *Scotland*

Loch Tulla. Woods about Killin. Achrioch and other woods around Tyndrum. Glen Fallock (B.B.S. 1929).

*Perthshire*: (Wheldon, 1915).

### *Ireland*

Cushendall (B.B.S. 1928), Killarney (B.B.S. 1935), Ventry.

Scattered information has been gleaned from the Reports of the British Bryological and Mycological Societies, from Dixon (1924), Macvicar (1910, 1912), Mayfield (1930), Duncan (1924) and from the personal remarks of many bryological and lichenological friends.

### ADJUSTMENTS IN RESPECT TO DISTRIBUTION

In a northern wood we should not expect to find the same flora as in a southern wood of the same type. The general flora would be similar but some species occurring in the former would be absent or rarer than in the latter and

*vice versa*. Variations in the flora also occur according to the eastern or western situation of the wood. Therefore the correct interpretation of the general list which follows depends partly on adjustments in respect to distribution for some species which are given below. Those with a western, northern or southern preference are indicated by W, N or S respectively.

### *Bryophytes*

- |                                      |                                   |
|--------------------------------------|-----------------------------------|
| Acrobolbus wilsoni (W)               | Lepidozia pinnata (W)             |
| Adelanthus decipiens (W)             | L. trichoclados (W and N)         |
| Anastrepta orcadensis (W and N)      | Leptodon smithii (S)              |
| Aneura latifrons (N and W)           | Leptoscyphus cuneifolius (W)      |
| A. palmata (N and W)                 | L. taylori (N and W)              |
| Anoetangium compactum (N and W)      | Lophozia bantriensis (N)          |
| Anomodon longifolius (N and W)       | L. floerkii (N)                   |
| Aplozia atrovirens (N)               | L. muelleri (N and W)             |
| Bazzania triangularis (W)            | L. porphyroleuca (N)              |
| B. tricenata (W)                     | Madotheca cordeana (W and N)      |
| B. trilobata (W)                     | M. porella (SW)                   |
| Blepharostoma trichophyllum (W)      | M. thuja (W and N)                |
| Blindia acuta (N)                    | Marsupella funkii (N and W)       |
| Breutelia arcuata (N and W)          | Metzgeria conjugata (N and W)     |
| Bryum filiforme (N and W)            | M. hamata (W)                     |
| B. provinciale (S)                   | M. pubescens (N)                  |
| Campylopus schwarzii (N and W)       | Mnium orthorrhynchum (W)          |
| C. setifolius (N and W)              | Nowellia curvifolia (N)           |
| Cololejeunea calcaria (W)            | Odontoschisma denudatum (N)       |
| C. rossettiana (W)                   | Oligotrichum hercynicum (N)       |
| C. microscopica (W and N)            | Orthodontium gracile (N and W)    |
| Colura calyptrifolia (NW)            | O. heterocarpum (N)               |
| Dicranodontium longirostre (N and W) | Orthothecium intricatum (N and W) |
| Dicranum fuscescens (N)              | O. rufescens (N and W)            |
| D. uncinatum (N)                     | Pedinophyllum interruptum (N)     |
| Drepanolejeunea hamatifolia (W)      | Plagiochila punctata (W and N)    |
| Eremomotus myriocarpus (NW)          | P. spinulosa (W and N)            |
| Eurhynchium circinatum (S)           | P. tridenticulata (W and N)       |
| E. striatulum (S)                    | Pleurozia purpurea (N and W)      |
| Fissidens osmundoides (N)            | Preissia quadrata (N and W)       |
| Frullania fragilifolia (W)           | Ptilidium pulcherrimum (N)        |
| F. germana (W and N)                 | Radula aquilegia (W)              |
| F. microphylla (W)                   | R. lindbergiana (N and W)         |
| Grimmia hartmani (N and W)           | R. voluta (W)                     |
| G. patens (N)                        | Rhabdoweisia crenulata (N)        |
| G. retracta (N and W)                | Saccogyna viticulosa (N and W)    |
| Harpalejeunea ovata (W)              | Scapania aequiloba (N and W)      |
| Harpanthus scutatus (N)              | S. cuspiduligera (N)              |
| Herberta hutchinsia (W)              | S. umbrosa (N and W)              |
| Hygrobiella laxifolia (N)            | Sematophyllum demissum (W)        |
| Hylacomium umbratum (NW)             | S. micans (W)                     |
| Hylacomium flagellare (N and W)      | Sphenolobus exsectus (W)          |
| Hypnum callichroum (N and W)         | S. hellerianus (W)                |
| H. cristacastrensis (N and W)        | S. minutus (N)                    |
| H. eugyrium (N and W)                | S. ovatus (W and N)               |
| Jamesoniella autumnalis (W)          | Thuidium delicatulum (W and N)    |
| Jubula hutchinsia (W)                | Ulotia drummondii (N and W)       |
| Lejeunea flava (SW)                  | U. ludwigii (N and W)             |
| L. holtii (SW)                       | Webera elongata (N and W)         |
| L. maevicari (SW)                    | W. tozeri (S)                     |
| L. patens (N)                        |                                   |

### *Lichens*

- |                                 |                          |
|---------------------------------|--------------------------|
| Anthracothecium hibernicum (SW) | Arthopyrenia laburni (W) |
| Arthonia aspersella (SW)        | Arthopyreniaceae (S*)    |
| A. excipienda (SW)              | Aspicilia lacustris (W)  |
| A. pruinata (S)                 | Bacidia effusa (S)       |

*Bacidia phacodes* (S)  
*Biatora micrococca* (W)  
*B. tenebricosa* (W)  
*Biatorina atropurpurea* (S)  
*B. globulosa* (S)  
*Bilimbia albidocarpa* (SW)  
*B. naegelii* (S)  
*Buellia praecavenda* (S)  
*Clathroporina calcarea* (SW)  
*Dermatocarpon aquaticum* (W)  
*Enterographa crassa* (S)  
*Ephebe lanata* (W)  
*Ephebeia hispidula* (W)  
*Graphidales* (S\*)  
*Graphina ruiziana* (SW)  
*Lecanactis abietina* (S)  
*L. premnea* (S)  
*Lecania dubitans* (W)  
*Lecanora epanora* (N)  
*Leptogidium dendriticum* (SW)  
*Leptogium burgessii* (W)  
*L. cretaceum* (S)  
*L. diffractum* (SW)  
*L. fragrans* (S)  
*L. palmatum* (SW)  
*L. ruginosum* (SW)  
*L. tremelloides* (SW)  
*Lithographa dendrographa* (SW)  
*Lobaria* (W\*)  
*Lobarina scrobiculata* (S)  
*Menegazzia pertusa* (W)  
*Microthelia micula* (SW)  
*Nephromium* (W\*)  
*Normandina pulchella* (W)  
*Ochrolechia tartarea* (N)  
     var. *subtartarea* (S and W)

*Opegrapha leightonii* (S)  
*O. viridis* (S)  
*Parmelia dubia* (S)  
*Parmeliella atlantica* (SW)  
*P. plumbea* (W)  
*Parmeliopsis hyperopta* (N)  
*Pannaria rubiginosa* (W)  
*Peltidea aphthosa* (N and W)  
*Phaeographis lyellii* (SW)  
*Phlyctis agelaea* (S)  
*P. argena* (S)  
*Physcia elaeina* (S)  
*Platysma chlorophyllum* (W)  
*Polychidium muscicolum* (W)  
*Porina carpinea* (S)  
*P. lectissima* (W)  
*P. leptalea* (W)  
*Porinaceae* (S\*)  
*Ramalina pollinaria* (S)  
*Rhizocarpon viridiatrum* (W)  
*Rinodina exigua* (S)  
*R. roboris* (S)  
*Solorina saccata* (W)  
*Sphaerophorus* (W\*)  
*Squamaria gelida* (N)  
*Staurothele rupifraga* (W)  
*Stenocybe bryophila* (W)  
*S. hyssacea* (W)  
*S. septata* (S)  
*Stictina* (W\*)  
*Thelidium sparsulum* (SE)  
*T. viride* (SW)  
*Thrombium cretaceum* (SE)  
*Toninia caradocensis* (S)  
*Verrucaria parva* (SW)

S\* —most members have some southern preference.

W\*—all the species have a western preference.

#### LIST OF BRYOPHYTES AND LICHENS OCCURRING IN BRITISH WOODS

*Nomenclature.* As in Part I.

*Arrangement of the list.* The first eleven columns refer to the occurrence of bryophytes and lichens in the following woods.

- (1) Oak woods in which *Quercus sessiliflora* is dominant.
- (2) Oak woods in which *Q. robur* is dominant.
- (3) Heathy oak woods.
- (4) Birch woods. The corticolous plants are not necessarily on birch.
- (5) Coniferous woods, especially pine. The corticolous plants do not necessarily occur on conifers.
- (6) Ash woods.
- (7) Ash scrub.
- (8) Ash-oak woods.
- (9) Alder woods (carr generally).
- (10) Beech woods (general but not acidic). These are included so as to make the list comprehensive. The frequency symbol will often be identical with that given in the general list of Part I for the beech woods of the chalk plateaux, but not necessarily so.
- (11) Oak-beech woods.

The frequency indicators are as in Part I, with the following emendations, which apply equally to Part I. When a space is left blank the species may be regarded as normally

absent. In Part I a blank was said to indicate that the species was definitely absent. This is too decided a statement about small plants which can be so easily overlooked and are often somewhat plastic in respect of habitat. The presence of a dash (—) indicates that the species is probably present and presumably rare. The habitat indications in the last column are as in Part I. "Damp" includes wet places such as beds of streams. As the habitat for so many liverworts must be described as damp, the indicator is used only for those of decidedly wet situations. "Nitrophilous" indicates that the species is usually more abundant at the margins and where nitrogenous matter (bird-droppings, etc.) is present. A few other indications of particular habitat are given but these are self-explanatory.

Oak woods are treated as *Quercus sessiliflora* and *Q. robur* woods. The peculiar oak woods of Symonds Yat and Muckcross (pp. 464-5, 467-8) on limestone have been listed separately as oak-beech woods, and heathy oak woods also have a separate column. There has been an endeavour made to produce a list which is general for the type of wood and exceptional features pertaining to certain woods have had to be neglected. For instance, a false idea of the *Q. sessiliflora* wood would be given by including in the list the calcicolous plants of the woods at Muckcross, Aymestry or Symonds Yat. Similarly the *Q. robur* woods of the eastern borders of Dartmoor (p. 465) have had to be treated with a certain amount of reserve.

MOSSES	<i>Q. sessiliflora</i>	<i>Q. robur</i>	Heathy oak	Birch	Conifer	Ash	Ash scrub	Ash-oak	Alder	Beech	Oak-beech	Habitat and notes
<i>Amblystegium confervoides</i>						r.	r.			r.	v.r.	Ground, stones
<i>A. filicinum</i>	r.	o.				f.	o.	o.		f.	o.	Ground. Damp
<i>A. juratzkanum</i>	o.	o.			—	o.	o.	o.	o.	r.	—	Ground
<i>A. serpens</i>	o.	o.		o.	—	o.	f.	o.	o.	f.	a.	Ground
<i>A. varium</i>	r.	r.		r.					o.	—		Bases, ground. Damp
<i>Anomodon attenuatus</i>	v.r.				—				v.r.			Stones, (bases)
<i>A. longifolius</i>	r.	—				o.	o.	—	r.	v.r.	v.r.	Stones
<i>A. viticulosus</i>	o.	o.				f.	a.	o.	o.	o.-f.	a.	Bases, stones
<i>Atrichum undulatum</i>	s.d.	a.	a.	f.	a.	f.	f.	f.-a.	o.	f.	a.	All but trunks
<i>Aulacomnium androgynum</i>	o.	o.	o.	l.a.	o.	—	—	—	o.		r.	Ground, (bases)
<i>A. palustre</i>	f.	o.	f.	f.	f.	r.	o.	o.	o.-f.			Ground. Damp
<i>Barbula cylindrica</i>	v.r.	o.			v.r.	f.	a.	o.		o.	o.	Banks, (stones)
<i>B. fallax</i>	o.	o.	o.	—	v.r.	a.	a.	f.		o.	a.	Banks
<i>B. rubella</i>	o.	o.	o.	r.	v.r.	f.	a.	o.		o.-f.	f.	Banks, stones
<i>B. unguiculata</i>	r.	o.	r.	—	r.	f.	f.	o.		o.	a.	Banks, stones. Margins
<i>Bartamia halleriana</i>	o.											Stones. Damp
<i>B. pomiformis</i>	o.	—	o.	o.	—			—				Banks, (stones)
<i>Brachythecium glareosum</i>	o.	o.	—	—	—	o.	o.	o.		r.-o.	f.	Banks, stones
<i>B. plumosum</i>	f.	o.	—	—	—	o.	o.	o.	—	—	o.	Stones. Damp
<i>B. populeum</i>	o.	o.	—	—	—	o.	o.	o.		o.	f.	Banks, stones
<i>B. purum</i>	a.	o.	a.	a.	a.	o.	o.	a.	f.	o.-f.	f.-a.	Ground
<i>B. rivulare</i>	o.	f.	r.	—	—	f.	f.-a.	o.-f.	o.-f.	r.	o.	All but trunks. Damp
<i>B. rutabulum</i>	a.	a.-d.	a.	f.	f.	a.	a.	f.-a.	o.-f.	f.	a.	All but trunks
<i>B. starkii</i>	r.		r.	—	—							Stones
<i>B. velutinum</i>	f.	a.	r.	o.	—	f.	f.	f.	—	o.-f.	f.	All
<i>Breutelia arcuata</i>	f.	—	—	o.	—	r.	—	—	r.	—	—	Banks
<i>Bryum capillare</i>	o.	a.	a.	o.	o.	a.	a.	f.	o.	o.-f.	o.	All but trunks
<i>B. pallens</i>	o.	r.-o.	o.	o.	—	o.	o.	o.	—	r.	—	Ground. Damp
<i>B. provinciale</i>	—	—				r.	o.	—		r.	r.	Banks, stones
<i>B. roseum</i>	o.	o.	o.	—	r.	—	—	o.	o.		v.r.	Banks
<i>Buxbaumia aphylla</i>	l.	r.	r.		l.							Ground, (bases)
<i>B. indusiata</i>			r.		l.							Bases
<i>Camptothecium lutescens</i>		r.				o.	f.	r.		o.	r.	Banks, ground. Margins
<i>C. sericeum</i>	r.	r.-o.		v.r.		f.	a.	o.	v.r.	o.	o.	All but trunks
<i>Campyllum chrysophyllum</i>		r.				f.	f.	o.		o.	r.	Ground, banks, stones
<i>C. hispidulum</i>						o.	f.	—		o.-f.	o.	Stones, (bases)
var. <i>sommerfeltii</i>												
<i>C. riparium</i>	o.	o.	o.	o.	—	—		o.	f.	r.	—	All but trunks
<i>Campylopus flexuosus</i>	f.	o.	a.	f.	f.	v.r.		o.	—	v.r.	o.	Ground, (bases)
<i>C. fragilis</i>	o.	r.	o.	o.	f.	v.r.		r.	—		o.	All but trunks
<i>C. pyriformis</i>	f.	r.	f.-a.		f.-a.	v.r.		r.	—		o.	Banks, ground

Mosses contd.	<i>Q. sessilifl.</i>	<i>Q. robur</i>	Heathy oa	Birch	Conifer	Ash	Ash scrub	Ash-oak	Alder	Beech	Oak-beech	Habitat and notes
<i>Ceratodon purpureus</i>	a.	o.	a.	f.	f.	o.	o.	o.	o.	o.	—	Ground, banks. Margin
<i>Climacium dendroides</i>	o.	r.	—	o.	r.	—	—	—	f.	—	o.	Ground. Damp
<i>Cryphaea heteromalla</i>	o.	o.	—	—	—	o.-f.	o.-f.	o.	—	r.	o.	Trees. Elder
<i>Dichodontium pellucidum</i>	o.	r.	—	o.	r.	o.	r.	r.	—	v.r.	r.	Stones. Damp
<i>Dicranella heteromalla</i>	a.	o.-f.	a.	f.-a.	a.	o.	o.	f.	o.	o.	f.	All
<i>D. rufescens</i>	o.	o.	—	—	—	o.	o.	o.	—	r.	r.	Ground. Damp
<i>D. schreberi</i>	o.	o.	—	—	—	—	—	o.	—	r.	o.	Ground, banks
<i>D. varia</i>	r.	o.	o.	—	—	r.	o.	o.	o.	—	—	Ground, banks. Damp
<i>Dicranodontium longirostre</i>	l.f.	—	—	—	—	—	—	—	—	—	—	All but trunks
<i>Dicranoweisia cirrata</i>	o.	o.	o.	o.	o.	o.	o.	o.	—	o.	r.	All
<i>Dicranum bonjeani</i>	o.	r.	o.	o.	r.	r.	o.	r.	—	r.	o.	Ground, banks
<i>D. flagellare</i>	—	o.-l.f.	—	o.	o.	—	—	—	—	—	—	Bases, (ground)
<i>D. majus</i>	a.-s.	o.	r.	—	o.	o.	o.	o.	—	r.	v.r.	Banks
<i>D. montanum</i>	—	o.	—	o.	o.	—	—	—	o.	—	—	Banks, stones. Damp
<i>D. scoparium</i>	a.	f.	a.	a.	a.	a.	a.	f.	o.	o.-a.	o.	All
<i>D. spurium</i>	r.	r.	r.	r.	—	—	—	r.	r.	—	—	Banks. Damp
<i>D. uncinatum</i>	r.	—	r.	—	r.	—	—	—	—	—	—	Stones
<i>D. undulatum</i>	o.	—	r.	o.	o.	—	—	—	—	—	—	Ground, banks
<i>Ditrichum flexicaule</i>	v.r.	v.r.	—	—	—	f.	a.	o.	—	f.	l.	Ground, (stones)
<i>Drepanocladus aduncus</i>	r.	r.	l.f.	o.	l.	—	—	l.	o.	—	—	Ground. Damp margin
<i>D. commutatus</i>	o.	f.	—	o.	—	f.	—	o.	o.	r.-o.	o.	Ground. Damp margin
<i>D. exannulatum</i>	o.	r.	l.f.	o.	l.	—	—	—	r.	—	—	Ground. Damp margin
<i>D. fluitans</i>	o.	r.	l.f.	o.	l.	—	—	—	o.	—	—	Ground. Damp margin
<i>Encalypta streptocarpa</i>	r.	r.	—	—	—	f.	a.	r.	—	r.-o.	f.	Banks, stones. Margin
<i>Eurhynchium abbreviatum</i>	r.	o.	—	—	—	o.	o.	o.	—	o.-f.	o.	Banks, stones
<i>E. circinatum</i>	—	r.	—	—	—	o.	f.	r.	—	o.	f.	Stones. Margins
<i>E. confertum</i>	o.	o.	—	o.	—	o.	f.	f.	—	o.-f.	f.	Bases, banks, stones
<i>E. crassinervium</i>	r.	o.	—	—	—	f.	f.	o.	—	o.-f.	f.	Banks
<i>E. curvisetum</i>	—	o.	—	—	—	o.	o.	o.	—	r.	—	Ground, stones. Damp
<i>E. murale</i>	o.	o.	—	—	—	o.	o.	o.	—	o.-f.	—	Stones
<i>E. myosuroides</i>	a.	o.	f.	f.	l.	o.	f.	o.	—	o.-f.	f.	Bases, stones
<i>E. myurum</i>	f.	o.	f.	—	—	o.	f.	f.	o.-f.	o.	—	Bases, (stones)
<i>E. piliferum</i>	o.	o.	—	—	—	o.-f.	o.	o.	r.	o.	f.	Bases, ground, banks
<i>E. praelongum</i>	a.	a.-s.d.	f.	f.	o.	a.	a.	a.	f.	o.-f.	a.	All but trunks
<i>var. stokesii</i>	f.-a.	o.	o.	o.	o.	o.	o.	o.	o.	r.	o.	All but trunks
<i>E. pumilum</i>	o.	o.-f.	—	—	—	o.	o.	o.	—	o.	o.	Ground, (stones)
<i>E. rusciforme</i>	f.	f.	l.	o.	o.	f.	o.	o.	o.	o.	o.	Ground. Damp
<i>E. speciosum</i>	—	r.	—	—	—	—	—	o.	o.	r.	—	All but trunks. Damp
<i>E. striatulum</i>	r.	—	—	—	—	o.-f.	f.	r.	—	r.	o.	Stones
<i>E. striatum</i>	f.-a.	f.	o.-f.	o.	o.	f.-s.d.	f.	a.	o.	f.	a.	All but trunks
<i>E. swartzii</i>	o.	o.-f.	o.	r.	—	f.	a.	o.	o.	o.-f.	a.	Ground. Margins
<i>E. tenellum</i>	—	r.	—	—	—	f.	f.	r.	—	o.	o.	Stones
<i>Fissidens adiantoides</i>	f.	r.	o.	o.	—	o.-f.	f.	o.	—	r.	—	Banks, stones. Damp
<i>F. bryoides</i>	o.	f.	o.	—	—	o.	o.	f.	—	o.-f.	o.	Banks, ground
<i>F. decipiens</i>	r.	r.	—	—	—	o.	o.-f.	o.	—	o.-f.	f.	Stones. Damp
<i>F. exilis</i>	r.	r.	—	—	—	—	—	—	—	r.	r.	Ground, banks
<i>F. taxifolius</i>	o.	a.	o.	o.	o.	f.	f.	f.	—	f.	f.-a.	Ground, banks
<i>Funaria calcaria</i>	v.r.	r.	—	—	—	o.	f.	r.	—	r.	r.	Stones. Margins
<i>F. ericetorum</i>	o.	r.	o.	—	—	o.	—	—	—	r.	r.	Ground, banks
<i>F. hygrometrica</i>	o.	o.	o.	o.	o.	o.	o.	o.	—	o.-l.f.	o.	Ground, banks, stones
<i>Grimmia apocarpa</i>	—	r.	—	—	—	f.	a.	r.	—	l.f.	f.	Stones. Margins
<i>G. montana</i>	—	r.	—	—	—	—	—	—	—	—	v.r.	Stones
<i>Heterocladium heteropterum</i>	f.	o.	—	r.	r.	o.	—	o.	—	v.r.	v.r.	Stones. Damp
<i>Homalia trichomanoides</i>	o.	o.	o.	—	r.	o.	o.	r.	o.	o.	o.	Trees, stones
<i>Hylocomium brevirostre</i>	o.	o.	—	—	—	o.	o.	—	—	o.	o.	Banks, stones
<i>H. loreum</i>	a.	o.	f.	—	f.	r.	r.	o.	—	o.	o.	Banks, stones
<i>H. splendens</i>	a.	o.	a.	a.	f.-a.	o.	f.	f.	—	r.-o.	o.	Banks, (stones)
<i>H. squarrosum</i>	f.	o.-f.	a.	f.	a.	o.	f.	o.	o.	o.	o.	Ground. Margins
<i>H. triquetrum</i>	a.	a.	a.	o.	f.	a.	a.	f.-a.	—	f.	a.	Ground, banks
<i>H. umbratum</i>	o.	—	r.	—	—	—	—	—	—	—	—	Banks, (stones)
<i>Hyocomium flagellare</i>	a.	o.	—	—	o.	—	—	r.	—	—	—	Stones. Damp
<i>Hypnum cristacastrensis</i>	f.	r.	o.	o.	f.	—	—	—	—	—	—	Banks, stones
<i>H. cordifolium</i>	o.	o.	o.	o.	—	—	—	o.	f.	—	—	Ground. Damp
<i>H. cupressiforme</i>	a.	a.	a.	f.	a.	a.	a.	a.	f.	a.	a.	All
<i>var. ericetorum</i>	f.-a.	f.	a.	f.-a.	f.-a.	o.	o.	f.	o.	v.r.	f.	Ground
<i>var. filiforme</i>	a.	a.	f.	f.	a.	o.	f.	f.	f.	a.	f.	Trunks
<i>var. tectorum</i>	r.	o.	o.	—	—	o.	f.-a.	o.	—	r.	o.	Banks
<i>H. cuspidatum</i>	l.f.	l.f.	l.f.	l.f.	l.	a.	o.	f.	a.	r.	o.	Ground. Damp
<i>H. giganteum</i>	o.	r.	o.	—	—	—	—	—	—	—	—	Ground. Damp

Mosses contd.	<i>Q. sessiflora</i>	<i>Q. robur</i>	Heathly oak	Birch	Conifer	Ash	Ash scrub	Ash-oak	Alder	Beech	Oak-beech	Habitat and notes
<i>Hypnum molluscum</i>	o.	o.				d.	d.	o.		f.	f.	Ground, banks, stones
<i>H. patientiae</i>	o.	o.		—		o.		r.		r.	o.	Ground, banks, stones
<i>H. schreberi</i>	a.	o.-f.	a.	a.	f.-a.	o.	o.	f.		r.	r.	Ground, banks. Margins
<i>Leptodon smithii</i>	r.	o.				r.		r.				Trunks
<i>Leucobryum glaucum</i>	f.-a.	o.	a.	f.	f.	v.r.		v.r.			o.	Ground, (bases)
<i>Leucodon sciurioides</i>	o.	o.	—	r.	r.	o.		r.-o.	o.	o.	f.	Trunks
<i>Mnium affine</i>	o.	o.		o.		a.	o.	o.		o.	o.	Ground, banks
<i>M. cuspidatum</i>	f.	o.	r.	r.	r.	a.	a.	f.	o.	o.	r.	Bases, ground, banks
<i>M. hornum</i>	a.-s.	o.-f.	a.	f.	o.-f.	a.	a.	a.	f.	f.	a.	Bases, ground, banks
<i>M. punctatum</i>	f.-a.	f.	f.	f.	o.-f.	f.		f.	f.	o.	o.	Ground. Damp
<i>M. riparium</i>	v.r.					r.			—	v.r.	v.r.	Ground, stones. Damp
<i>M. rostratum</i>	o.	o.-f.		r.	r.	a.	a.	f.	r.	f.	o.	Banks, stones
<i>M. stellare</i>	r.	f.				f.	f.	r.	—	o.	o.	Banks, stones
<i>M. undulatum</i>	a.	a.-s.d.	o.	f.	o.	a.	f.	f.-a.	o.	o.-f.	f.	Bases, ground, banks
<i>Neckera complanata</i>	a.	f.-a.	f.-a.	f.		a.	a.	a.	f.	o.-f.	f.	Trunks, bases, stones
<i>N. crispa</i>	v.r.	r.				f.	a.	r.		o.	o.	Stones, (bases)
<i>N. pumila</i>	o.	o.		o.		f.	f.	f.	—	f.	f.	Trunks
<i>Orthodontium heterocarpum</i>	o.		o.									Ground, (bases)
<i>Orthotrichum affine</i>	o.	f.	o.	o.	r.	o.	f.	f.		o.	o.	Trunks
<i>O. anomalum</i> var. <i>saxatile</i>	v.r.	r.				o.	a.	r.		r.-o.	r.	Stones. Margins
<i>O. leiocarpon</i>	a.	o.	o.	—	—	o.	o.	o.		—	—	Trunks
<i>O. lyellii</i>	a.	f.	—	o.	—	o.	f.	f.		o.	o.	Trunks
<i>O. pulchellum</i>	o.	o.	o.	o.		o.	o.			r.		Trunks
<i>Plagiothecium denticulatum</i>	a.	o.-f.	f.	f.	—	a.	a.	o.	o.	o.	a.	Ground, banks, (bases)
<i>P. depressum</i>	r.	r.				o.				v.r.	o.	Ground, stones, (bases)
<i>P. elegans</i>	f.	o.	f.-a.	f.	o.	r.		r.		r.	r.	Ground, banks
<i>P. latebricola</i>	o.	o.				o.		o.		r.		Bases, ground. Damp
<i>P. silesiacum</i>	r.				r.				r.			Bases
<i>P. silvaticum</i>	a.	f.-a.	f.-a.	o.	—	a.	a.	o.	o.	o.	r.	Bases, ground
<i>P. undulatum</i>	a.	o.	f.	f.	f.-a.	o.		o.		—	—	Banks, (stones)
<i>Pleuridium subulatum</i>	o.	r.-o.	f.	o.	o.	v.r.	v.r.	v.r.		r.	o.	Ground, banks
<i>Polytrichum aloides</i>	f.-a.	r.	a.	—	—	v.r.	r.	o.		—	f.	Banks
<i>P. commune</i>	l.a.	l.	l.	l.f.	l.a.				f.			Ground. Damp
<i>P. formosum</i>	a.	a.	a.	l.a.	l.a.	r.	o.	o.		o.	r.	Ground, banks
<i>P. gracile</i>	f.	r.	f.	o.	f.	v.r.		r.		r.		Ground, banks
<i>P. juniperinum</i>	f.	r.-o.	a.	f.	—	v.r.	r.-o.	r.-o.		v.r.	o.	Ground, banks. Margins
<i>P. nanum</i>	o.	r.	o.	—	—	—		r.		—	r.	Ground, banks
<i>P. piliferum</i>	f.	r.	a.	—	—	v.r.	r.	r.				Ground, banks. Margins
<i>Porotrichum alopecurum</i>	l.f.	f.	—	o.	o.	a.	a.	f.	—	f.	f.	Ground, banks, stones
<i>Pottia recta</i>	r.		r.							r.	r.	Ground. Margin
<i>Pterygophyllum lucens</i>	f.	o.		o.	o.	v.r.		v.r.		—		Banks, (stones). Damp
<i>Rhabdoweisia crenulata</i>	o.	r.	o.	—	—							Stones
<i>Rhaconitrium lanuginosum</i>	o.		o.-f.	r.	r.		r.					Stones. Margin
<i>Seligeria paucifolia</i>												Stones
<i>S. pusilla</i>						o.	o.			f.	v.r.	Stones
<i>S. recurvata</i>	o.	r.								v.r.	v.r.	Stones
<i>Sematophyllum demissum</i>	r.											Stones. Damp
<i>S. micans</i>	r.											Stones. Damp
<i>Sphagnum cymbifolium</i>	l.a.	l.	l.a.	l.f.	l.a.			l.r.	l.f.			Ground. Damp
var. <i>squarrosulum</i>	a.	o.	a.	f.	l.			r.				Ground. Damp
<i>S. plumulosum</i>	l.a.	l.o.	l.	l.	l.	v.r.		v.r.				Ground. Damp
<i>S. quinquefarium</i>	a.	o.	l.f.	f.	l.f.	v.r.		l.				Ground. Damp
<i>S. recurvum</i>	l.f.	l.f.	l.f.	l.f.	l.f.	v.r.		l.f.	l.f.			Ground. Damp
<i>S. squarrosum</i>	l.f.	r.	—	o.	—							Ground. Damp
<i>Tetraphis pellucida</i>	a.	r.	a.	f.	f.	v.r.		r.		o.		Bases, banks
<i>Thuidium delicatulum</i>	f.	r.			l.							Ground. Damp
<i>T. philiberti</i>	r.	r.-o.				o.	f.	r.		r.	r.	Ground, banks, stones
<i>T. recognitum</i>	r.	r.				o.	o.-f.	r.		r.	r.	Ground, banks, stones
<i>T. tamariscinum</i>	a.	a.	a.	f.	f.	a.-s.	f.	f.-a.		f.	a.	All
<i>Tortula laevipila</i>	o.	o.	o.	o.		r.	o.	o.		f.	o.	Trunks
<i>T. subulata</i>	o.	o.	o.			o.	f.	o.		o.-f.	o.	Banks, Margins
<i>Trichostomum tortuosum</i>	o.	r.		r.		f.	a.	r.		o.-f.	o.	Banks, stones
<i>Ulota bruchii</i>	f.	o.	r.	o.-f.	—	o.	o.	f.	o.	o.	o.	Trunks
<i>U. crispa</i>	f.	o.	o.	o.	o.	o.	o.	f.	o.	o.-f.	o.	Trunks
<i>U. ludwigii</i>	o.	r.	r.	o.	o.			r.				Trunks
<i>U. phyllantha</i>	o.-f.	o.	o.	—	—				o.	r.	o.	Trunks, stones
<i>Webera albicans</i>	f.	o.	l.f.	—	—	r.	r.	o.		r.		Ground. Damp
<i>W. carnea</i>	o.	f.				o						Ground, banks. Damp
<i>W. nutans</i>	o.-f.	o.	a.	o.-f.	o.	v.r.		r.		v.r.	r.	Ground, (bases)



MOSSES <i>contd.</i>	<i>Q. sessiliflora</i>	<i>Q. robur</i>	Heathly oak	Birch	Conifer	Ash	Ash scrub	Ash-oak	Alder	Beech	Oak-beech	Habitat and notes
<i>Weisia calcarea</i>			r.	r.	r.	o.					f.	Stones
<i>W. curvirostris</i>	o											Stones. Damp
<i>W. microstoma</i>	o.	o.				o.	o.-f.	f.		o.	r.	Ground, banks, stones. Margins
<i>W. rupestris</i>	o.	r.		o.				r.			r.	Stones
<i>W. tenuis</i>		r.-o.				o.		o.		r.-o.	v.r.	Stones
<i>W. verticillata</i>	r.	r.				f.	r.	r.		r.	r.	Stones. Damp
<i>W. viridula</i>	o.	o.				o.	o.	o.		o.	o.	Ground, banks. Margins
<i>Zygodon conoideus</i>	f.	o.			o.					r.	o.	Trunks
<i>Z. forsteri</i>	r.									v.r.		Trunks
<i>Z. viridissimus</i>	f.	f.	o.			o.	f.	o.		f.	r.	Trunks, (stones)
LIVERWORTS												
<i>Acrobolbus wilsoni</i>	r.											Trunks. Stones. Damp
<i>Adelanthus decipiens</i>	o.											Stones, (bases). Damp
<i>Alicularia scalaris</i>	f.-a.	r.-o.	a.	f.	l.a.		v.r.	o.			r.	Banks, stones
<i>Anastrepta oreadensis</i>	o.			o.	o.							Banks, stones
<i>Aneura palmata</i>	o.-f.	r.	o.	o.	r.				r.	r.	r.	Bases, ground
<i>Anthoceros humoti</i>	o.-f.	r.		r.					r.			Banks
<i>Aplozia crenulata</i>	f.-a.	o.	f.-a.	o.	o.	o.	r.	o.		r.	r.	Banks
<i>A. pumila</i>	o.	r.	l.	o.	l.	r.		r.	r.			Banks, stones. Damp
<i>A. riparia</i>	f.	o.	—	o.	—	r.		o.	—	r.	o.	Ground. Damp
<i>Bazzania trilobata</i>	f.	r.	f.-a.	f.	f.-a.							Ground, banks, stones
<i>Calypogeia arguta</i>	f.-a.	o.	o.	o.	o.			o.			r.	Banks
<i>C. fissa</i>	a.	o.	o.-f.	o.	o.	r.	r.	o.	o.	o.-f.	o.	Ground, banks
<i>C. trichomanis</i>	a.	a.	a.	f.	f.-a.				o.-f.		r.	Ground, banks
<i>Cephalozia bicuspidata</i>	a.	f.	f.	a.	l.f.	o.	r.	o.-f.	a.	r.	o.	Ground, banks
<i>C. connivens</i>	o.		f.	a.	l.f.				f.			Ground, banks. Margins
<i>C. media</i>	a.	r.	f.	o.-f.	o.-f.	v.r.		r.			r.	Bases, ground, banks
<i>Chiloscyphus pallescens</i>	r.	o.				r.		r.		o.	—	(Ground)
<i>C. polyanthus</i>	f.	o.				r.		r.				Ground, banks, stones. Damp
<i>Cololejeunea calcarea</i>	r.	r.		r.		o.	o.	r.		r.	r.	Ground, banks, stones.
<i>C. microscopica</i>	o.	r.		o.		o.	o.	r.		—	—	Stones, (trunks)
<i>C. rosettiana</i>		v.r.				o.	o.	r.		r.	o.	Ground, banks, stones
<i>Colura calyptrifolia</i>	o.				r.							Stones, (trunks). Damp
<i>Conocephalum conicum</i>	o.	a.			—	r.		o.-f.				Banks, stones. Damp
<i>Diplophyllum albicans</i>	a.-d.	o.-f.	a.	a.	a.	r.	r.	o.		v.r.	o.	All but trunks
<i>Drepanolejeunea hamatifolia</i>	o.-f.	r.		o.		r.		r.			r.	Stones, trunks. Damp
<i>Eucalyx hyalinus</i>	o.-f.	r.	o.	o.	—			r.		v.r.	r.	Ground, banks, stones
<i>Frullania dilatata</i>	f.-a.	f.-a.	o.	a.	o.	f.-a.	f.	f.-a.	f.	f.	f.	Trunks, (stones)
<i>F. fragilifolia</i>	o.-f.	r.	—	o.	r.			v.r.				Trunks, stones
<i>F. tamarasci</i>	a.	f.	f.	f.	f.	f.	f.	f.-a.	o.	o.	o.	All
<i>Gymnocolea inflata</i>	o.	r.	f.-a.	f.	o.	v.r.		r.	o.			Banks, stones, ground. Margins
<i>Harpalejeunea ovata</i>	o.	r.		o.		r.		r.			r.	Trunks, stones
<i>Harpanthus scutatus</i>	o.	r.	r.	o.								All but trunks
<i>Jamesoniella autumnalis</i>	l.f.											Bases, stones
<i>Jubula hutchinsia</i>	o.-f.	r.						r.				Stones. Damp
<i>Lejeunea cavifolia</i>	f.	o.	o.	o.	—	o.-f.	f.	o.	o.	o.	o.	All but trunks
<i>L. diversiloba</i>	r.											Banks
<i>L. flava</i>	o.											All but trunks. Damp
<i>L. holtii</i>	o.											Stones. Damp
<i>L. macvicari</i>	r.											Trunks. Damp
<i>L. patens</i>	o.	r.		o.								All but trunks. Damp
<i>Lepidozia pinnata</i>	r.		o.	r.	r.							Banks, stones
<i>L. reptans</i>	a.	o.	a.	a.	a.	r.	r.	o.		v.r.	r.	All but trunks
<i>L. setacea</i>	f.	o.	o.	f.	f.				o.			All but trunks. Damp
<i>L. sylvatica</i>	r.	v.r.					v.r.					Ground, banks. Damp
<i>Leptosciaphus anomalus</i>	o.	o.	f.	o.-f.	o.				o.			Bases, stones
<i>L. cuneifolius</i>	r.			o.	r.							Bases, stones
<i>L. taylori</i>	f.		f.-a.	f.	f.							Bases, stones. Margins
<i>Lophocolea bidentata</i>	o.-f.	o.	f.	f.-a.	f.-a.	o.	o.	o.	o.	o.-f.	o.	Banks, ground, stones
<i>L. cuspidata</i>	a.	a.	f.	o.	o.-f.	a.	a.	f.-a.	o.	f.-a.	o.	All but trunks
<i>L. heterophylla</i>	o.-f.	o.	f.	o.	f.-a.	o.-f.	o.	o.	r.	f.-a.	o.	Bases, ground, banks
<i>Lophozia attenuata</i>	f.	o.	o.	o.	o.-f.	o.		o.	r.	v.r.		Bases, banks, stones
<i>L. badensis</i>	o.					o.-f.			o.	o.		Banks. Damp. Margins
<i>L. floerkii</i>	f.	o.	f.-a.	f.	f.				o.	o.	r.	Ground, stones. Margins

LIVERWORTS <i>contd.</i>	<i>Q. sessiliflora</i>	<i>Q. robur</i>	Heathly oak	Birch	Conifer	Ash	Ash scrub	Ash-oak	Alder	Beech	Oak-beech	Habitat and notes
<i>Lophozia incisca</i>	o.	r.	o.	o.-f.	—			r.	r.			All
<i>L. muelleri</i>	r.	o.		r.-o.	v.r.	o.		r.		r.		All but trunks. Margins
<i>L. quinqueidentata</i>	f.	r.	o.	o.		r.	r.					All but trunks
<i>L. turbinata</i>	r.	o.-f.		r.	v.r.	f.		o.	o.	o.-f.	a.	Banks. Damp. Margins
<i>L. ventricosa</i>	f.	o.	f.	f.	f.			r.-o.	o.			All but trunks
<i>Lunularia cruciata</i>	r.	a.		r.-o.	—	f.	o.-f.	r.	r.	o.	o.	Paths. Damp
<i>Madotheca laevigata</i>	o.	o.				f.	o.-f.	r.		r.-o.	o.	Trees, stones
<i>M. platyphylla</i>		r.				f.	a.	r.		o.-f.	o.-f.	Trees, stones. Margins
<i>Marchesinia mackaii</i>	—	r.				o.-f.	o.	r.		r.	o.-f.	Stones
<i>Marsupella emarginata</i>	f.	r.	f.	f.	o.-f.	r.		r.				All but trunks
<i>Metzgeria conjugata</i>	f.	r.	r.	f.	o.			r.		r.	o.	Stones, (trunks)
<i>M. furcata</i>	a.	o.-f.	f.	f.	o.-f.	a.	f.	f.	f.	f.	f.	Trunks, (stones)
<i>M. hamata</i>	r.			r.	r.							Stones. Damp
<i>M. pubescens</i>						o.	o.			o.	r.	Stones
<i>Microlejeunea ulicina</i>	f.	o.	r.	f.	r.	f.	o.	f.		o.-f.	o.	Trunks
<i>Nowellia curvifolia</i>	o.-f.		o.	f.	o.-f.							Bases
<i>Odontoschisma denudatum</i>	o.	r.	o.	o.	—			r.				Bases, ground. Margins
<i>O. sphagni</i>	o.	r.	l.	o.	l.							Ground. Damp. Margins
<i>Pellia epiphylla</i>	f.	o.	l.	f.	l.f.	r.		o.	f.	v.r.	r.	Ground, banks, stones.
												Damp. Margins
<i>P. fabbrioniana</i>	r.	f.				o.	l.	o.	o.-f.	f.	o.	Ground, banks. Damp.
												Margins
<i>Plagiochila asplenoides</i>	a.	f.	f.	f.	a.	a.	f.	f.	o.	o.-f.	a.	All but trunks
<i>P. punctata</i>	f.	r.	o.	a.	o.	v.r.		r.			o.	Trees, bases, stones
<i>P. spinulosa</i>	f.	r.	o.	f.		v.r.		r.			o.	All
<i>P. tridenticulata</i>	o.-f.			r.	r.						r.	Trees, stones
<i>Preissia quadrata</i>	o.	r.		o.		f.	f.	o.		v.r.	r.	Banks. Damp
<i>Ptilidium ciliare</i>	o.		f.-a.	o.	o.-f.							Ground
<i>P. pulcherrimum</i>	r.		r.	r.	v.r.				v.r.			Trunks, bases
<i>Radula aquilegia</i>	o.			r.								Stones, trees. Damp
<i>R. carringtonii</i>	l.f.										r.	Stones
<i>R. complanata</i>	o.-f.	o.	o.	o.	r.	o.	o.-f.	o.		o.	o.	Trees, stones
<i>R. holtii</i>	r.											Stones. Damp
<i>R. voluta</i>	o.		l.		r.							Banks, stones. Damp
<i>Reboulia hemisphaerica</i>	v.r.	r.				o.	f.	r.		r.	r.	Banks
<i>Riccia glauca</i>	o.	r.	r.			r.		o.		r.	r.	Ground. Path
<i>Ricciocarpus natans</i>	r.	r.	o.	o.					r.			Ground. Damp
<i>Saccogyna viticulosa</i>	f.-a.	o.	o.	o.	r.-o.	o.		r.-o.	r.			Ground, banks
<i>Scapania aequiloba</i>	r.	r.	r.			o.	o.-f.	r.				Banks, stones
<i>S. aspera</i>	v.r.	r.				a.	a.	r.-o.		o.	o.	Banks, stones
<i>S. compacta</i>	o.	r.	o.-f.	o.	f.-a.	v.r.	v.r.	r.		r.		Ground
<i>S. curta</i>	o.	o.	o.	r.	r.	o.	o.	o.		r.	r.	Ground, banks. Margins
<i>S. cuspiduligera</i>	v.r.					o.	o.	r.				Banks, stones
<i>S. gracilis</i>	a.	o.	f.	a.	f.	o.	o.-f.	o.		r.		Banks, stones
<i>S. irrigua</i>	o.	o.	o.	r.	r.	r.	r.	o.		r.	r.	Ground, banks. Margins
<i>S. nemorosa</i>	f.-a.	o.	f.	f.	f.	o.-f.	o.-f.	o.		r.	r.	All but trunks
<i>S. umbrosa</i>	f.	o.	f.	f.	f.	r.	r.	r.				All but trunks
<i>Sphenolobus exsectaeformis</i>	o.	r.	o.-f.	o.	r.-o.	r.	r.	r.				Trunks, banks
<i>S. hellerianus</i>	r.		—	r.	r.							Trunks
<i>S. ovatus</i>	o.		o.	f.	r.							Trunks, stones
<i>Trichocolea tomentella</i>	o.-f.	o.		o.	—	o.	o.	o.		r.	r.	Ground, banks. Damp
LICHENS												
<i>Acrocordia biformis</i>	f.	o.-f.	—	o.-f.		f.	f.	f.	—	r.	o.	Trunks
<i>A. epipolaea</i>		r.				o.	f.	r.		r.	f.	Stones
<i>A. gemmata</i>	f.	f.	—	o.		f.	f.	f.	r.	r.-o.	o.	Trunks
<i>Alectoria jubata</i>	f.	o.-f.	f.	f.	f.-a.	r.	r.	r.				Trunks. Conifers
<i>Allarthonia patellulata</i>	r.		r.		r.	r.	r.		r.			Trunks
<i>Anaptychia ciliaris</i>	r.	o.	r.	r.	r.	f.	f.	o.		r.	o.	Trunks
<i>Arthonia aspersa</i>	r.	r.	—			r.	r.	r.				Trunks
<i>A. aspersella</i>	o.	r.				r.	r.	r.		r.		Trunks
<i>A. didyma</i>	r.	r.	—		—	o.	o.	r.	r.	r.		Trunks
<i>A. gregaria</i>	o.	o.	—		—	o.	o.	o.		r.-o.		Trunks
<i>A. lurida</i>	o.	o.	—		r.	o.	o.	o.	r.	r.	r.	Trunks
var. <i>spadicea</i>	o.	o.	—		r.	o.	o.	o.	r.	r.	r.	Trunks
<i>A. pruinata</i>	o.-f.	o.				o.	f.	o.-f.				Trees. Margins
<i>A. punctiformis</i>	r.	r.				r.		r.				Trees
<i>A. radiata</i>	f.	f.	f.			f.	f.	f.	o.	r.	o.	Trees
var. <i>swartziana</i>	a.	a.	a.			a.	a.	a.	f.	o.	f.	Trees

LICHENS *contd.*

	<i>Q. sessiliflora</i>	<i>Q. robur</i>	Heathy oak	Birch	Conifer	Ash	Ash scrub	Ash-oak	Alder	Beech	Oak-beech	Habitat and notes
<i>Arthopyrenia analepta</i>	o.	r.		r.	—			r.	—	r.	r.	Trees
<i>A. cinereopruinosa</i>	r.	o.				r.	o.	o.	—	r.	r.	Trees
<i>A. epidermidis</i>	f.	f.	f.	o.		o.	o.	f.	o.	r.-o.	o.	Trees
<i>A. fallax</i>	f.-a.	o.	f.-a.	o.-f.	—	r.	o.	f.	—	r.	o.	Trees
<i>A. laburni</i>	r.	r.	r.					r.	r.			Trees
<i>A. punctiformis</i>	o.	o.	o.	r.-o.		o.	o.	o.	f.	r.	r.	Trees
<i>A. rhyponia</i>	r.	r.			o.	r.		r.	—			Trees
<i>A. saxicola</i>						r.	r.-o.			r.	o.	Stones
<i>A. stigmatella</i>	o.-f.	o.		r.				o.	—			Trees
<i>A. submicans</i>	o.	r.		o.			o.		o.	o.	o.	Trees
<i>Aspicilia calcarea</i>		r.										Trees
<i>A. lacustris</i>	f.	r.		r.	r.		f.	r.		r.	o.	Stones. Margins
<i>Bacidia arceutina</i>	o.	o.	r.		v.r.	o.	o.	o.	r.	o.	o.	Stones. Damp
<i>B. atrogrisea</i>	f.	o.	o.	r.	v.r.	o.	f.	o.	r.	o.	o.	Trees, (stones)
<i>B. beckhausii</i>	r.	r.-o.		r.		r.	r.	r.	r.	r.	r.	Trees. Margins
<i>B. effusa</i>	o.	r.				o.	o.	o.		r.-o.	r.	Trees
<i>B. incompta</i>	o.	r.	r.	r.	v.r.	f.	f.	o.		r.	r.	Trees
<i>B. inundata</i>	o.	o.				o.		o.	o.			Stones. Damp
<i>B. luteola</i>	o.	o.	o.		v.r.	o.	o.	o.		o.		Trees
<i>B. phacodes</i>	o.	o.	o.	r.-o.	r.	f.	f.	f.	r.	o.	o.	Trees
<i>B. salicifolia</i>	r.				r.				r.			Trees
<i>Baeomyces rufus</i>	o.	r.	f.	o.	o.			r.			o.	All but trunks. Margins
<i>Biatora bauschiana</i>	o.		r.		r.			o.				Stones
<i>B. coarctata</i>	o.	o.	o.	r.	r.	o.	o.	o.		r.	o.	Stones. Margins
<i>B. flexuosa</i>	r.	o.	o.	o.	o.-f.	r.	r.	o.	—	r.	r.	Bases. Conifers
<i>B. fuliginea</i>	o.	o.	o.	o.	o.	o.	o.	o.	—	—		Bases. Margins
<i>B. fusciorubens</i>		v.r.				o.	f.	r.		r.	o.	Stones. Margins
<i>B. granulosa</i>	o.	r.	f.-a.	o.	o.		r.	r.		r.	r.	Ground, (bases). Margins
<i>B. immersa</i>		r.				o.	f.	r.		r.	o.-f.	Stones. Margins
<i>B. micrococca</i>	r.	r.			o.	r.	r.	r.				Trees, bases.
<i>B. quereia</i>	o.	o.	o.			o.	o.	o.		o.	o.	Trees, bases. Margins
<i>B. tenebricosa</i>	r.	v.r.							r.			Trees, bases
<i>B. turgidula</i>	r.	r.	o.	o.	o.				—	r.	r.	Trees, bases.
<i>B. uliginosa</i>	o.	r.	o.-f.	o.	r.			r.				Ground. Margins
<i>B. vernalis</i>	o.	o.		o.	—	v.r.			—			Trees, bases, (ground)
<i>B. viridescens</i>	o.	r.	o.	o.	o.	r.		o.	r.		r.	Bases, (ground). Margins. Conifers
<i>Biatorella pinicola</i>					r.				—			Trees. Conifers
<i>B. pruinosa</i>		r.				o.	f.	r.		r.	o.	Stones. Margins
<i>Biatorina atropurpurea</i>	o.-f.	r.		r.	o.		o.	o.	—			Trees
<i>B. erysiboides</i>	r.	r.			o.	o.	o.	r.				Trees, bases, ground. Conifers
<i>B. globulosa</i>	r.			v.r.	v.r.			r.				Trees
<i>B. graniformis</i>	o.	o.		r.	r.				r.			Bases. Margins
<i>B. griffithii</i>	o.	o.	o.	o.	o.	f.	f.	f.	r.	r.	o.	Trees
<i>B. lenticularis</i>	r.	o.		o.	o.	f.	a.	r.	r.		f.-a.	Stones. Margins
<i>B. lightfootii</i>	f.	r.	o.	f.	o.	r.	r.	r.	r.	r.	r.	Trees
<i>B. prasina</i>	r.	r.	o.	r.	o.	o.	o.	r.	f.			Trees, bases, ground
<i>B. pulvereae</i>	o.-f.	r.	o.	r.	r.	r.	r.	r.	—	r.	r.	Bases, (trees), (ground)
<i>B. spodiza</i>					r.							Trees
<i>Bilimbia albidocarmea</i>						r.	o.				r.	Stones
<i>B. chlorococca</i>	r.				r.-o.				r.			Trees
<i>B. naegeli</i>		r.			—	o.	o.	o.	r.	r.	r.	Trees, bases. Margins
<i>B. nitschkeana</i>	r.	r.	r.	r.	r.	r.	r.	r.	r.			Bases
<i>B. sabuletorum</i>	o.	o.	o.	r.	r.	o.	f.	o.		o.	o.	Stones. Margins
<i>Botrydina vulgaris</i>	f.-a.	f.	a.	f.-a.	f.-a.	r.	o.	o.	o.	r.-o.	r.	Ground, banks
<i>Buellia disciformis</i>	o.	r.	o.	o.	r.	r.	r.	r.	—	r.	r.-o.	Trees, bases
<i>B. myriocarpa</i>	o.	f.	f.	f.	f.	a.	a.	f.	o.	f.		Trees, bases, stones
<i>Calicium curtum</i>	f.	o.	o.	o.	o.	o.	o.	o.	r.	r.	o.	Trees, bases. Margins
<i>C. hyperellum</i>	f.	f.	o.	o.	o.	o.	o.	f.	r.	r.	o.	Trees, bases
<i>Callopiisma cerinum</i>	o.	o.	o.	r.	r.	o.	o.	o.	o.	r.	o.	Trees, bases. Margins
<i>C. citrinum</i>		r.				o.	f.	r.		r.		Stones. Margins
<i>Candelariella vitellina</i>	o.	o.				o.	o.	o.			o.	Stones. Margins, nitrophilous
<i>Catinaria grossa</i>	o.	r.				o.	o.	o.		r.	r.	Trees
<i>Chaenotheca chrysocephala</i>	o.	r.		o.	o.	o.				r.	r.	Trees, bases
<i>C. melanophaea</i>	r.		o.		o.	r.				r.	r.	Trees, bases. Conifers
<i>Cladonia sylvatica</i>	f.	o.	a.	o.	o.				o.			Ground, banks. Margins

LICHENS contd.	<i>Q. sessiliflora</i>	<i>Q. robur</i>	Heathy oak	Birch	Conifer	Ash	Ash scrub	Ash-oak	Alder	Beech	Oak-beech	Habitat and notes
<i>Cladonia caespiticia</i>	f.	o.	o.	o.	r.	r.		o.		r.	f.	All but stones
<i>C. cervicornis</i>	f.	r.	f.	o.	o.		o.	o.			f.	Ground, banks, stones. Margins
<i>C. coccifera</i>	f.	o.	f.-a.	f.	f.	r.	o.	o.	o.		f.	Ground, banks. Margins
<i>C. crispata</i>	o.	r.	f.	o.	o.	r.	o.		o.	r.	o.	Ground, banks, stones. Margins
<i>C. digitata</i>	f.	o.	o.	—	—	—	—	—			r.	Ground, banks
<i>C. fimbriata</i>	a.	f.	a.	o.-f.	o.-f.	f.	f.-a.	f.		r.-o.	o.	Bases, ground, banks
var. <i>subulata</i>	a.	f.	a.	o.-f.	f.	f.	f.	f.	o.	r.-o.	o.	Bases, ground, banks
<i>C. flabelliformis</i>	a.	a.	a.	—	—	o.	f.	f.		r.	o.	Bases, ground, banks
<i>C. floerkeana</i>	o.	r.	f.	o.	o.			r.				All but trunks. Margins
<i>C. furcata</i>	f.	f.	f.-a.	f.	f.	r.	f.	o.	r.	r.	o.	Ground, banks. Margins
<i>C. gracilis</i>	o.-f.	o.	f.	o.-f.	o.-f.						r.	Ground, banks. Margins
<i>C. macilentia</i>	a.	a.	a.	f.	f.	o.	f.	f.	—	r.	f.	Bases, ground, banks
<i>C. ochrochloria</i>	f.-a.	o.-f.	f.-a.	f.	f.	o.	o.	o.	f.	o.	o.	Bases, ground, banks
<i>C. parasitica</i>	o.	o.	o.					o.		r.	—	Bases, (banks)
<i>C. pityrea</i>	f.	o.	f.	o.	o.			o.	—			Bases, ground, banks
<i>C. pyxidata</i>	f.	o.	f.	f.	f.	r.	o.	o.	o.	r.-o.	f.	All but trunks. Margins
var. <i>poecila</i>	v.r.	r.				o.	a.	o.		o.	o.	Banks. Margins
<i>C. rangiformis</i>	o.	f.		o.		f.	f.-a.	f.		o.	f.	Ground, banks. Margins
<i>C. squamosa</i>	a.	f.	f.	f.	f.	o.	o.	f.	f.	r.	f.	All but trunks
<i>C. subsquamosa</i>	f.	o.	o.			o.					o.	All but trunks
<i>Clathroporina calcarea</i>						r.	r.				r.	Stones
<i>Coenogonium ebeneum</i>	f.	o.		o.		r.						Stones
<i>Collema granuliferum</i>	r.	r.				o.	a.	r.		o.	a.	Stones. Margins
<i>C. multifidum</i>	r.	r.				o.	f.	r.		o.	f.	Stones. Margins
<i>C. pulposum</i>	r.	r.				f.	a.	o.		r.-o.	o.	Ground, banks, stones. Margins
<i>C. terrulentum</i>						r.						Trunks
<i>Dermatocarpon aquaticum</i>	f.	o.	—									Stones. Damp
<i>D. minutum</i>	r.	r.				f.	a.	r.			o.	Stones. Margins
<i>Diploicia canescens</i>	r.	r.				o.	f.	r.	r.	r.	r.-o.	Trunks, bases, stones. Margins
<i>Enterographa crassa</i>	f.-a.	f.-a.	f.		r.	f.	f.	f.		o.-f.	o.-f.	Trunks
<i>Evernia prunastri</i>	a.	f.	f.	f.	a.-d.	f.	f.	a.	f.	o.	o.	Trunks
<i>Gongylia viridis</i>	r.									r.		Ground, banks. Margins
<i>Graphina anguina</i>	o.	o.						o.		r.		Trunks
<i>G. ruiziana</i>	r.	o.		o.								Trunks
<i>Graphis elegans</i>	f.	f.	o.	o.	r.	f.	f.	f.		f.-a.	f.	Trunks
<i>G. scripta</i>	f.	f.	o.	f.	r.	a.	a.	a.	r.	f.	f.	Trunks
<i>Gyalecta carneolutea</i>	—	o.				o.	o.-f.	o.				Trunks, (stones)
<i>G. cornea</i>	o.	r.					r.	r.	v.r.	r.	r.	Trunks
<i>G. cupularis</i>	r.	r.				o.	f.	r.		o.	o.	Stones. Margins
<i>G. flotovii</i>	o.	o.				o.	o.	o.		r.	r.	Trunks
<i>G. truncigena</i>	o.	o.				o.	o.	o.		v.r.	o.	Trunks
<i>Hypogymnia physodes</i>	a.	f.	a.	f.	f.-a.	a.	a.	f.	f.	f.	f.	Trunks, bases, (stones)
<i>Lecanactis abietina</i>	f.	o.-f.	f.	o.	f.	o.	o.	o.		r.		Trunks
<i>L. premea</i>	f.	o.	f.			o.	o.	o.				Trunks
<i>Lecania dubitans</i>	r.				r.	r.						Trunks, bases
<i>Lecanora allophana</i>	o.-f.	o.-f.	f.	r.	r.	f.	f.	f.	r.	r.	o.	Trunks
<i>L. carpinea</i>	o.	o.	o.	r.	r.	o.	f.	o.	f.	o.	o.	Trunks, bases. Margin
<i>L. chlorina</i>	f.-a.	a.	f.	o.-f.	o.	a.	a.	f.	f.	f.	f.	Trunks
<i>L. conizaea</i>	o.-f.	o.	f.	o.	o.	r.	r.	r.		o.	o.	Trunks
<i>L. conizaeoides</i>	f.	o.	f.	f.	f.	o.	o.	o.		o.	o.	Trunks, bases. Conifers
<i>L. expallens</i>	f.	o.-f.	f.	o.	a.	r.	r.-o.	r.-o.	o.	o.	o.	Trunks, bases. Conifers
<i>L. hageni</i>	o.	o.	o.	r.	r.	o.	o.	o.	r.	o.	o.	Trunks
<i>L. intumescens</i>	o.	o.	o.	r.	r.	o.	o.	o.	o.	o.	o.	Trunks
<i>L. pallida</i>	f.	o.-f.	o.	r.	r.	o.	o.-f.	o.	o.	o.	o.	Trunks, bases. Margins
<i>L. piniperda</i>	v.r.		v.r.			r.						Trunks, bases. Conifers
<i>L. rugosa</i>	o.	r.-o.	o.	o.	o.	o.	o.	f.	o.	r.	o.	Trunks
<i>L. subfusca</i>	f.	f.	f.	r.	r.	f.	f.	f.	r.	r.	o.	Trunks
<i>L. symmicta</i>	o.-f.	o.	o.	o.	o.	o.	o.	o.		r.-o.	o.	Trunks, bases
<i>L. symmictera</i>	r.-o.	r.	o.	r.	r.	r.	r.	o.	r.	r.	r.	Trunks, bases. Margins
<i>L. varia</i>	f.	o.	f.	f.	f.	r.	r.	o.	r.	r.	o.	Trunks, bases
<i>Lecidea contigua</i>	o.	r.	o.	r.							r.	Stones. Margins
<i>L. crustulata</i>	r.	r.	o.		r.			r.		r.		Stones. Margins
<i>L. dicksonii</i>	o.		o.	r.	r.							Stones. Margins
<i>L. parasema</i>	f.-a.	f.-a.	f.-a.	o.	o.	a.	a.	a.	f.	o.-f.	f.	Trunks, bases

LICHENS contd.	<i>Q. sessiliflora</i>	<i>Q. robur</i>	Heath oak	Birch	Conifer	Ash	Ash scrub	Ash-oak	Alder	Beech	Oak-beech	Habitat and notes
<i>Lecidea soreidiza</i>	o.	r.	o.	r.	r.			r.			r.	Stones. Margins
<i>L. sylvicola</i>	o.	o.	o.	o.	o.			o.				Stones. Margins
<i>Leptogium burgessii</i>	o.											Trunks
<i>L. diffractum</i>						r.	o.					Stones. Margins
<i>L. fragile</i>						r.	o.					Stones. Margins
<i>L. fragrans</i>		r.				o.	o.	r.		r.	r.	Stones. Margins
<i>L. lacerum</i>	r.	o.	v.r.	v.r.		f.	f.	f.		o.	o.	All
var. <i>pulvinatum</i>		r.				r.	a.	r.			o.	Stones, (banks)
<i>L. massiliense</i>						r.	o.-f.					Stones
<i>L. microscopicum</i>	r.	r.				o.	o.-f.	o.			r.	Stones. Margins
<i>L. minutissimum</i>						r.	o.-f.	r.			—	Banks
<i>L. schraderi</i>		r.				o.	a.	r.		r.	o.	Banks, stones. Margins
<i>L. sinuatum</i>	r.	r.				o.	o.	r.			r.	Stones, (banks)
<i>Leptorhaphis carrollii</i>	r.	r.		r.		o.	o.					Trunks
<i>L. epidemidis</i>	r.		r.	o.				r.	r.			Trunks
<i>Lithographa dendrographa</i>	o.	r.										Trunks
<i>Lobaria laciniata</i>	o.	r.-o.										Trunks
<i>L. laetevirens</i>	o.-f.	o.				r.-o.	r.	r.		r.	o.	Trunks
<i>L. pulmonaria</i>	f.	o.	r.	r.	r.	r.-o.	r.-o.	o.		r.	o.	Trunks
<i>Lobaria scrobiculata</i>	o.	o.			v.r.					r.	r.	Trunks, stones
<i>Melanotheca gelatinosa</i>	o.			r.		r.		o.		r.		Trunks
<i>Menegazzia pertusa</i>	o.			o.	o.				r.	r.	r.	Trunks
<i>Microphiale diluta</i>	o.	r.	r.	r.	f.	v.r.	v.r.	r.		r.	r.	Trunks, bases. Conifers
<i>Microthelia micula</i>	r.-o.	r.			v.r.	r.			r.		r.	Trunks
<i>Mycoblastus sanguinaria</i>	o.	r.	r.	o.-f.	o.-f.							Trunks, bases
<i>Mycoporum quercus</i>	r.-o.	r.				r.				r.	r.	Trunks, bases, stones
<i>Nephromium laevigatum</i>	r.			r.	r.				r.			Bases, stones
var. <i>parile</i>												
<i>N. lusitanicum</i>	f.	o.-f.		r.								Bases, trunks, stones
<i>Normandina pulchella</i>	o.	r.	r.	r.	r.	r.	r.	r.-o.	r.	r.	r.	Trunks
<i>Ochrolechia tartarea</i>	f.	o.	f.	f.	f.	r.	r.	o.				Trunks, (stones)
var. <i>subtartarea</i>	a.	o.	a.	r.	r.	o.	o.	o.		r.-o.	o.	Trunks, (stones)
<i>O. parella</i>	r.	r.	o.	r.	r.	r.	o.	r.				Stones, (trunks). Margins
var. <i>turneri</i>	o.	o.	o.	o.	o.	o.	o.	o.	r.	o.	o.	Trunks
<i>Opegrapha atra</i>	f.	f.		o.		a.	a.	a.	o.	r.	f.	Trunks. Margins
<i>O. betulina</i>	o.	o.				f.	f.	o.		r.-o.	o.	Trunks, bases
<i>O. herpetica</i>	o.	o.				o.	o.	o.	—	r.-o.	o.	Trunks
<i>O. leightonii</i>		r.				o.	o.	o.				Stones
<i>O. varia</i>	f.	f.	f.	o.	o.-f.	a.	a.	a.	o.	r.	o.	Trunks. Margins
<i>O. viridis</i>		o.			r.	o.	o.	r.	r.			Trunks
<i>O. vulgata</i>	f.	f.	f.	o.	f.	a.	a.	a.	o.	r.-o.		Trunks. Margins
<i>Pannaria rubiginosa</i>	o.	o.	o.			r.	r.	r.			o.	Trunks, (stones)
var. <i>conoplea</i>	f.	f.	f.	r.	r.	r.	r.	r.	r.		o.	Trunks
<i>Parmelia caperata</i>	a.	a.	f.	r.-o.	r.	f.	f.	f.-a.	o.	f.	f.	Trunks, (stones)
<i>P. dubia</i>	f.	o.	o.	r.-o.	r.-o.	o.	o.	o.	o.	o.	o.	Trunks
<i>P. exasperata</i>	o.	r.	o.			r.		r.		—	—	Trunks
<i>P. fuliginosa</i>	o.	r.	o.	r.	r.	r.	r.	r.	r.	r.	r.	Trunks, bases, (stones)
var. <i>laetevirens</i>	a.	f.	o.	o.	o.	o.-f.	f.	a.	o.	f.	f.	Trunks, bases
<i>P. perlata</i>	f.	o.	f.	r.	r.	o.	o.	f.	r.	o.	o.	Trunks
<i>P. revoluta</i>	a.	o.	f.	o.	o.-f.	f.	f.	f.	r.	f.	f.	Trunks
<i>P. saxatilis</i>	a.	f.-a.	a.	f.	f.	a.	a.	a.	f.	f.	f.	Trunks, stones
<i>P. subaurifera</i>	f.	o.	a.	o.	o.	o.	f.	o.	f.	o.	o.	Trunks, bases
<i>P. sulcata</i>	f.-a.	o.	f.	o.	o.	f.	f.	o.	f.	o.	o.	Trunks
<i>P. tiliacea</i>	o.	r.	o.	r.	r.			r.	r.	r.	r.	Trunks
<i>Parmeliella corallinodes</i>	o.	r.	o.	v.r.	v.r.	v.r.			r.		r.	Trunks
<i>P. microphylla</i>	o.	r.										Stones
<i>P. plumbea</i>	o.	o.								r.	o.	Trunks, stones
<i>Parmeliopsis ambigua</i>	r.		r.-o.	r.	o.	r.				v.r.		Trunks
<i>P. hyperopta</i>	r.-o.		r.-o.	r.	r.-o.							Trunks
<i>Peltidea apothosa</i>	o.		o.	o.	o.							Stones. Margins
<i>Peltigera canina</i>	a.	a.	f.		r.	f.	a.	a.	o.	o.	f.	All but trunks. Paths
<i>P. horizontalis</i>	f.	o.				f.	o.	o.		o.	o.	All but trunks. Paths
<i>P. polydactyla</i>	f.-a.	f.-a.	f.	o.	r.	f.	f.	a.	o.	o.	f.	All but trunks. Paths
<i>P. rufescens</i>	f.	f.	f.	o.	o.	f.	a.	f.	o.	o.	f.	All but trunks. Paths
<i>P. scutata</i>	o.	o.	o.			r.	o.	o.		r.	o.	Trunks, (stones)
<i>P. spuria</i>	o.	o.				o.	o.-f.	o.		r.	o.	Ground, banks. Margins
<i>Pertusaria amara</i>	a.	f.-a.	f.	f.	f.	a.	f.	a.	—	f.	f.	Trunks, (stones)
<i>P. carneopallida</i>									r.			Trunks

**LICHENS** *contd.*

LICHENS contd.	<i>Q. sessiliflora</i>	<i>Q. robur</i>	Heathy oak	Birch	Conifer	Ash	Ash scrub	Ash-oak	Alder	Beech	Oak-beech	Habitat and notes
<i>P. communis</i> (= <i>P. pertusa</i> )	f.	f.	f.	r.-o.		a.	f.	a.	—	f.	f.	Trunks, (stones)
<i>Pertusaria globulifera</i>	f.	f.	f.	r.-o.	r.	f.	f.	f.-a.	—	r.	r.	Trunks, (stones)
<i>P. leioplaca</i>	f.	a.	o.	r.-o.	r.	a.	f.	a.	—	o.	r.	Trunks
<i>P. multipluncta</i>	o.-f.	o.	o.	f.	r.	o.	o.	o.	—	r.	r.	Trunks
<i>P. velata</i>	o.	r.-o.	o.				r.	r.		r.		Trunks
<i>P. wulfenii</i>	a.	a.	f.	r.	r.	f.	f.	f.		o.-f.	f.	Trunks
<i>Petractis clausa</i>		v.r.				o.	f.	r.		r.-o.	o.	Stones. Margins
<i>Phaeographis dendritica</i>	o.	o.				o.	o.	o.		r.	r.	Trunks
<i>P. inusta</i>	o.	o.				o.	o.-f.	o.		o.	o.	Trunks
<i>Phlyctis agelaea</i>	a.	o.-f.	f.	r.	o.	o.	o.	f.	r.	f.	o.	Trunks
<i>P. argena</i>	a.	o.-f.	f.	r.	o.	o.	o.	f.	r.	r.	o.	Trunks
<i>Physcia alipolia</i> and vars.	o.	f.	o.	r.	r.	f.	f.	f.	r.	r.	o.	Trunks, stones. Margins
<i>P. claeina</i>	r.	o.	o.			o.	o.-f.	o.		o.	o.	Trunks. Margins
<i>P. grisea</i>	o.-f.	f.				o.	f.	o.	o.	o.	o.	Trunks, stones. Margins
<i>P. hispida</i> and vars.	f.	f.	o.	r.	o.	a.	a.	f.	f.	r.	f.	Trunks, bases, stones
<i>P. pulverulenta</i>	o.	f.	o.	r.	r.	f.	f.	f.	f.	o.	o.	Trunks, bases, (stones)
<i>P. virella</i>	r.	o.				o.	f.	o.	o.	r.	o.	Trunks, stones. Margins
<i>Placidium callosporum</i>	v.r.	r.				o.	f.	v.r.		r.	o.	Stones. Nitrophilous
<i>P. plicatum</i>							f.	r.		r.	o.	Stones. Nitrophilous
<i>P. murorum</i>		r.				o.	o.	f.		r.	o.	Stones
<i>P. xantholytium</i>						o.	f.			r.	o.	Stones. Nitrophilous
<i>Placynthium nigrum</i>		r.				o.	a.	r.		r.	o.	Trunks
<i>Platysma chlorophyllum</i>	o.		o.	o.	o.	r.				r.	o.	Trunks, (stones)
<i>P. glaucum</i>	a.	f.	f.	o.	o.	r.-o.	r.	f.		—	o.	Trunks
<i>P. pinastri</i>	v.r.		v.r.	r.	r.					—		Trunks
<i>Porina carpinea</i>	o.	f.				f.	f.	o.	o.	o.-f.	f.	Trunks
<i>P. chlorotica</i>	r.	r.		r.		r.	r.	r.		r.	o.	Stones. Margins
var. <i>linearis</i>						o.	o.	r.		r.	o.	Stones. Margins
<i>P. lectissima</i>	o.	r.								r.		Stones. Margins
<i>P. leptalea</i>	o.	r.	r.	r.	f.	r.	r.	r.		r.	r.	Trunks, bases. Conifers
<i>P. olivacea</i>	r.	r.				o.	o.	r.		r.	r.	Trunks
<i>Psora ostreata</i>	r.		r.	r.	r.-o.					v.r.		Bases, (trunks). Conifers
<i>P. lurida</i>		v.r.				o.	f.	v.r.		r.	o.	Stones. Margins
<i>Pyrenula nitida</i>	f.	f.	o.	o.		a.	a.	f.	o.	f.	o.	Trunks
var. <i>nitidella</i>	o.	o.	o.	o.		f.		f.	o.	f.		Trunks
<i>Racodium rupestre</i>	f.	o.	o.	o.	o.	r.	r.	r.				Stones. Margins
<i>Ramalina calicaris</i>	f.	f.	f.	o.	r.	f.	o.	a.	o.	o.	f.	Trunks
<i>R. farinacea</i>	f.-a.	f.-a.	f.-a.	f.-a.	a.	f.	a.	a.	o.	o.	f.	Trunks
<i>R. fastigiata</i>	f.-a.	f.-a.	f.-a.	f.	r.-o.	a.	a.	a.	o.	o.	f.	Trunks
<i>R. fraxinea</i>	f.	f.-a.	f.-a.	f.	r.	f.	f.-a.	f.-a.	f.-a.	o.	f.	Trunks
<i>R. pollinaria</i>	r.	o.	f.		r.	o.	o.	o.	o.	r.	r.	Trunks
<i>Rhizocarpon alboatrum</i> and varieties	o.	f.	o.	r.	r.	o.	f.	o.	r.	r.	o.	Trunks, (stones). Margins
<i>R. confervoides</i>	o.	r.	o.	o.	o.		v.r.	r.		r.		Stones. Margins
<i>R. viridiatrum</i>	o.	r.	r.		r.					o.		Stones. Margins
<i>Rinodina exigua</i>	r.	o.	o.	o.	o.	o.	o.	o.	o.	r.	o.	Trunks, bases. Margins
<i>R. isidioides</i>	r.				r.							Trunks
<i>R. roboris</i>	f.	f.	f.			o.	o.	o.			o.	Trunks
<i>R. sophodes</i>	r.-o.	r.-o.	o.			o.	o.	o.	o.			Trunks
<i>Solorina saccata</i>	r.	r.				o.	f.	r.			r.	Banks
<i>Sphaerophorus compressus</i>	o.	r.	o.	o.	o.							Stones. Margins
<i>S. globosus</i>	f.	r.	f.-a.	f.	f.							Stones, (bases). Margins
<i>Sphinctrina turbinata</i>	f.	o.	o.			o.	o.	f.		o.	o.	Trunks. Parasite
<i>Staurothele rupifraga</i>		v.r.				o.	f.	r.		r.	o.	Stones
<i>Stenocybe bryophila</i>	o.-f.	o.									r.	Trunks, bases. Hepatics
<i>S. byssacea</i>	r.	r.						r.	a.			Trunks. Alders
<i>S. septata</i>	f.	f.				o.	o.	o.				Trunks. Holly
<i>Stereocaulon nanum</i>	o.	o.	o.	—	—	—	—	o.				Stones. Margins
<i>Sticticia dufourii</i>	o.	r.										Trunks, stones
<i>S. fuliginosa</i>	a.	f.		r.-o.	r.	o.					o.	Trunks, stones
<i>S. limbata</i>	f.	o.-f.	o.							v.r.	r.	Trunks, stones
<i>S. sylvatica</i>	f.	f.				o.				r.	r.	Bases, stones
<i>Synechoblastus nigrescens</i>	o.	o.				o.	o.	o.		r.	o.	Trunks
<i>S. rupestris</i>	r.-o.					o.	f.	r.		r.	o.	Stones, (trunks)
<i>Teloschistes flavicans</i>	r.	r.	r.		r.	o.	o.	o.				Trunks
<i>Thelidium sparsulum</i>										o.		Stones. Chalk
<i>T. viride</i>	r.	r.				r.		r.		r.		Stones. Margins
<i>Thelotrema lepadinum</i>	f.	r.		o.-f.	—	r.		r.		r.	r.	Trunks, bases
<i>T. subtile</i>	r.											Trunks

LICHENS <i>contd.</i>	<i>Q. sessiliflora</i>	<i>Q. robur</i>	Heathy oak	Birch	Conifer	Ash	Ash scrub	Ash-oak	Alder	Beech	Oak-beech	Habitat and notes
<i>Thrombium cretaceum</i>		r.	—	—		o.	a.	r.		r.	o.	Stones. Chalk
<i>Toninia aromatica</i>		r.	—	—	o.							Stones
<i>T. caradocensis</i>	o.	r.	—	—	o.							Trees, bases. Conifers
<i>Usnea articulata</i>	o.	r.	o.	r.	r.	r.	r.	r.				Trunks
<i>U. ceratina</i>	a.	f.	a.	r.	f.	o.	f.	f.	o.	r.-o.	o.	Trunks
<i>U. dasypoga</i>	o-f.	o.	o.	r.-o.	r.	r.	r.	r.				Trunks
<i>U. florida</i>	f.	o.	f.	r.	r.	f.	o.	f.	o.	o.	o.	Trunks
<i>var. hirta</i>	f.	o.	f.-a.	o.-f.	o.	o.	f.	f.	o.	o.	f.	Trunks
<i>U. rubiginea</i>	f.	o.	f.	r.	r.	f.		f.				Trunks
<i>Verrucaria aethiobola</i>	f.	r.				r.		r.				Stones. Damp
<i>V. coerulea</i>	v.r.	r.				o.	o.-f.	r.			o.	Stones. Margins
<i>V. maculiformis</i>	r.	r.				r.	r.	—		o.	o.	Stones. Margins
<i>V. mutabilis</i>	v.r.						v.-r.			o.	r.	Stones. Margins
<i>V. nigrescens</i>		r.				o.	a.	r.		r.	o.	Stones. Margins
<i>V. parva</i>						r.	o.				r.	Stones. Margins
<i>V. rupestris</i>						r.	o.				o.	Stones. Margins
<i>V. sphinctrina</i>						r.	o.				o.	Stones. Margins
<i>V. viridula</i>	r.	r.				r.	o.	r.		r.	r.	Stones. Margins
<i>Xanthoria parietina</i>	r.	r.	o.	r.	r.	r.	f.	r.	r.	r.	o.	Trunks, bases, stones.
												Nitrophilous
<i>X. lychnea</i>	r.	r.	r.	r.	r.	o.	o.	o.	r.	r.	o.	Stones. Nitrophilous

#### "INCIDENTAL" OR "CASUAL" SPECIES

Some plants which are not usually of woodland habitat are included in the above list. They are frequent at the margins or in open places but occasionally occur in the actual wood. Those included do not comprise all such incidentals or casuals, though there has been some attempt at conformity in regard to their inclusion. Those which are frequent members of the heathy oak wood or the ash scrub or commonly incidental to other woods are included. Unless there is a special reason for doing so, plants which are rarely incidental to the woods are not given in the list but many of them are mentioned below.

#### Mosses

*Amblystegium fluviatile* and *irriguum* on stones in streams.

*Andraea crassinervia*, *petrophila* and *rothii* on rocks in open places of upland oak (*Q.s.*) woods.

*Anoetangium compactum* on damp rocks in open subalpine woods, birch at Tyndrum, oak (*Q.s.*) at Keskadale and Launchy.

*Antitrichia curtipendula* in upland oak as at Dolgelly, Keskadale and Wistmans.

*Barbula convoluta*, *hornschuchiana*, *recurvifolia* and *rigidula* in open woods, especially ash scrub.

*Blindia acuta*, on damp rocks in uplands.

*Brachythecium albicans*, *illecebrum* and *salebrosum*.

*Bryum bimum*, *caespitium* (scrub), *filiforme*, *inclinatorum* (scrub), *intermedium* and *pseudotriquetrum* (wet places).

*Campyllum elodes*, *polygamum* and *stellatum*, all in damp places.

*Campylopus atrovirens*, *setifolius* and *schwarzii* (Birkrigg), all in damp places.

*Cynodontium bruntoni* on subalpine rocks.

*Daltonia splachnoides*, very rare on shady rocks or trees.

*Dichodontium flavescens*, wet rocks.

*Dicranella cerviculata* (alder, oak), *squarrosa* (wet places in oak).

*Dicranum fuscescens* (birch, oak), *scottianum* (oak).

*Drepanocladus intermedium*, *revolvens*, *uncinatum*, all in wet places.

*Encalypta vulgaris*, ash scrub.

*Eurhynchium teesdalei* in wet places in ashwood.

*Fissidens incurvus*, *osmundoides* (wet places), *pusillus*, *viridulus*.

*Fontinalis antipyretica* and *squamosa* in wet places, the latter especially in streams in oak (Q.s.) woods.

*Funaria templetoni* on damp banks or rocks.

*Grimmia doniana* (screes in Q.s. woods), *hartmani* and *retracts* (on boulders in streams of Q.s. woods), *orbicularis* and *pulvinata* (in scrub).

*Heterocladium macounii* on damp rock faces in Q.s. wood.

*Hypnum callichroum* (subalpine Q.s.), *eugyrium*, *imponens*, *ochraceum scorpoides* and *stramineum*, all in wet places.

*Leptobryum pyriforme*, birch and alder.

*Leptodontium recurvifolium* on wet banks in Q.s. wood.

*Leskea polycarpa* on wet bases of trees.

*Mnium orthorrhynchum* and *subglobosum* in wet places.

*Oligotrichum hercynicum*, sandy or stony ground in uplands.

*Orthodontium gracile*, usually on rocks.

*Orthothecium rufescens* (oak, birch), *intricatum* (scrub).

*Philonotis fontana* in swamps of alder and other woods.

*Pleurochaete squarrosa* in ash scrub.

*Polytrichum urnigerum* in birch and oak woods.

*Sphagnum* species may be locally abundant in suitable situations in birch, oak or pine woods (see p. 474-5).

*Tetraphis browniana* on shaded sandstone rocks.

*Tortula intermedia* and *muralis* in ash scrub.

*Trichostomum crispulum* (ash scrub), *hibernicum* (oak), *mutabile* (ash and oak scrub), *nitida* (ash scrub), *tenuirostre* (oak).

*Ulota drummondii* in subalpine birch and oak.

*Webera annotina* in oak woods.

#### Liverworts

*Alicularia geoscypha*, in birch and oak woods.

*Aneura latifrons* (peaty woods), *major*, *multifida*, *pinguis* and *sinuata* all in wet places.

*Anthoceros husnoti* (oak and birch woods), *laevis* (on paths).



*Aplozia atrovirens* and *sphaerocarpa* in wet places.

*Bazzania tricenata* and *triangularis* have a similar distribution to that of *B. trilobata* but are rarer.

*Blepharostoma trichophyllum*, l.f. in Q.s. woods.

*Calypogeia neesiana* (rocks, etc.) and *succica* (damp logs).

*Cephalozia catenulata* and *leucantha* in birch and oak woods.

*Cephaloziella dentata*, *hampeana* and *starkii*, all on paths.

*Cololejeunea minutissima* on ash, yew, etc.

*Fossombronia caespitiformis*, *pusillus* and *wondraczeki* occasionally occur on paths.

*Frullania germana* and *microphylla* in birch and oak woods.

*Geocalyx graveolens* on shaded rocky banks.

*Herberta hutchinsia* on wet rocks in subalpine Q.s. woods.

*Jamesoniella carringtonii* in open birch and other woods.

*Lepidozia pearsoni* and *trichoclados*, on peaty banks.

*Lophozia bantriensis*, *barbata*, *porphyroleuca*.

*Madotheca cordeana* (oak), *porcella* (wet rocks in oak wood), *thuja*.

*Marchantia polymorpha*, damp places.

*Pedinophyllum interruptum* in ash scrub.

*Pleurozia purpurea* in boggy places of birch woods.

*Radula lindbergiana* in oak and birch woods.

*Riccia sorocarpa* (paths), *fluitans* (ditches and pools).

*Scapania dentata*, *intermedia*, *subalpina*, *undulata*, all in wet places in siliceous woods.

*Sphenolobus exsectus* on rocks in oak and other woods, *pearsoni* in shady ravines.

### *Lichens*

*Alectoria implexa* on trunks of firs.

*Arthonia astroidestera* and *exicipienda* in oak woods.

*Baeomyces roseus* in heathy woods.

*Biatora bauschiana* (stones), *mutabilis* and *viridescens* (firs, etc.).

*Biatorina pilularis* (upland woods), *synochea*.

*Bilimbia sphaeroides* on trees or ground.

*Buellia praecavenda* on holly and ash.

*Calicium quercinum* on stumps.

*Calloposma cerinellum* (elder), *lacteum* (ash scrub), *phloginum*, *pyraceum*.

*Candelaria concolor*, on trees.

*Cladonia uncialis* in heathy woods.

*Collema crispum*, *furvum*, *granosum* and *tenax*, all in ash scrub.

*Coniocybe furfuracea* on rocks or stony banks.

*Crocynia aeruginosa*, *finkii* (ash scrub), *flava*, *lanuginosa*.

*Dermatocarpon hepaticum* and *lachneum* in ash scrub.

- Diploschistes gypsaceus* and *scruposus* in scrub.  
*Ephebe lanata* and *Ephebeia hispidula* on wet boulders.  
*Evernia furfuracea* in upland woods.  
*Icmadophila ericetorum* in heathy woods.  
*Lecania cyrtella*, *erysibe* (ash scrub), *syringea*.  
*Lecanora polytropa* (on rocks), *sambuci* (on elders).  
*Lecidea albocoerulescens*, *cinerascens*, *jurana* (ash scrub) and *rivulosa*, all on rocks.  
*Leciographa parasitica* on *Ochrolechia* and *Pertusaria*.  
*Lemmopsis arnoldiana* on calcareous stones.  
*Lempholemma chalazanodes* and *myriococcum*.  
*Leptogidium dendriscum* on alder or in *Q.s.* woods.  
*Leptogium cretaceum* and *fragile* in ash scrub.  
*Microphiale lutea* on trees.  
*Ochrolechia pallescens* on trunks of trees.  
*Pachyphiale cornea* on smooth bark of trees.  
*Parmelia carporhizans*, *cetrata*, *cetrarioides*, *conspersa*, *crinita*, *omphalodes*, *scortea*.  
*Pertusaria leptospora*, *lutescens*, *pustulata*.  
*Phaeographis lyellii*, rare on trees (usually southern).  
*Psora lurida* in ash scrub.  
*Psorotrichia schaeferi* on calcareous rocks.  
*Ramalina evernioides*, chiefly on old oaks.  
*Solenopsora candicans* in ash scrub.  
*Squamaria crassa* in ash scrub, *gelida* in upland woods.  
*Staurothele ebborensis* in ash scrub.  
*Synechoblastus aggregatus* on trees.  
*Thalloidima candidum* and *coeruleonigricans* in ash scrub.  
*Thelidium immersum* and *incavatum* in ash scrub.  
*Verrucaria integra*, *muralis*, *parva*, *rupestris*, *sphinctrina*, all in ash scrub.  
*Usnea extensa* on trees.

#### OAK WOODS

In Somerset pedunculate oak woods are the more frequent and are on the deeper and less acidic soils. The *Quercus sessiliflora* woods are more prevalent on the shallower siliceous soils in the west of the county where the rainfall is higher. In many of them streams are abundant and deep combes or glens have been formed. The bed of the stream is strewn with boulders and on the sides of the combe the rock surface is often exposed. On the sloping banks (e.g. in Holford Combe) bryophytes are often more conspicuous than the phanerogams and ferns. *Dicranum majus*, *Mnium hornum*, *Dicranella heteromalla*, *Thuidium tamariscinum*, *Plagiothecium denticulatum*, *Hylocomium triquetrum* and *H. loreum* mask the mantle of *Oxalis*, *Stellaria holostea*, *Melampyrum*

*pratense*, *Vaccinium myrtillus* and *Blechnum*. In damper places on the rocky bank *Tetraphis pellucida*, *Cephalozia media*, *Calypogeia trichomanis*, *Diplophyllum albicans*, *Lophozia ventricosa* and *Lepidozia reptans* are associated; and any of them may become the dominant species. In marshy places bryophytes such as *Hypnum cuspidatum*, *Philonotis fontana* and *Polytrichum formosum* compete for dominance with *Anagallis tenella*, *Stellaria uliginosa*, *Chrysosplenium oppositifolium*, etc.

In the *Quercus sessiliflora* woods of the Silurian and Malvernian strata near Malvern (Salisbury and Tansley, 1921) which occur over both siliceous and calcareous rocks, the bryophytic flora of all the woods seems to be rather poor. Both mosses and liverworts appear to be more prevalent in the woods of the Malvernian rocks and of the May Hill sandstone than in the woods of the limestones. Considering the views put forward as to the conditions favourable to the dominance of *Q. robur* or *Q. sessiliflora* the authors say "with regard to the factor of soil depth, which Moss regarded as important in determining the dominance of *Q. robur* or *Q. sessiliflora*, it may be remarked that several of the limestone exposures show a soil depth adequate to support *Q. robur*, which does in fact occur but is very seldom dominant". Salisbury (1918) "concluded that the contrast with woods of *Q. robur* depends, at least partly, on a higher acidity, corresponding with a lower content of soluble mineral salts and of water". In regard to the Forest of Wyre Salisbury (1925) says "although *Q. sessiliflora* is the only oak on the higher parts of the forest, *Q. robur* (and *Q. robur*  $\times$  *Q. sessiliflora*) is found towards the foot of the slopes and on the alluvial flats. In parts of Ribbesford Wood under high forest, where the light intensity is low and the water content moderately high, a mossy vegetation occurs, recalling that characteristic of many *Q. sessiliflora* woods in North Wales. . . . A striking feature of the hepatic flora is that several species usually associated with the subalpine region have been recorded from Wyre Forest. These<sup>1</sup> include *Marsupella emarginata*, *Aplozia riparia*, *Plagiochila spinulosa*, *Lophozia quinquedentata* and *Blepharostoma trichophyllum*".

The dominance of *Quercus robur* or *Q. sessiliflora* does not appear to be dependent on one factor. It is certainly true that in British woods the latter is more abundant in the wetter hilly siliceous regions of the west. As a general rule the *Q. sessiliflora* woods are on siliceous soil, with boulders and stones strewn on the surface and with numerous rills and rivulets running down its slopes. In the *Q. sessiliflora* woods of east England and the Midlands these characters are much less pronounced, but from repeated statements by Salisbury (1916, 1918, 1921, 1925) in regard to such woods that they are richer in bryophytes, and especially in hepatics, than *Q. robur* woods in the same region, one must conclude that greater humidity prevails. In Kerry, where the humidity factor is a powerful one, *Q. sessiliflora* woods even extend over

<sup>1</sup> These species are certainly commoner in upland districts, but they occur at or near sea-level when the conditions are sufficiently humid and otherwise favourable.

a calcareous substratum.<sup>1</sup> On the shores of the Lower Lake at Muckcross where the underlying rock is carboniferous limestone, the corticolous bryophytes and lichens are similar to those of *Q. sessiliflora* woods on siliceous soil in other parts of the Killarney district, but the ground flora is less characteristic. In some places there is some resemblance to a Somerset wood of pedunculate oak, but generally the bryophytes and lichens, if we neglect those growing on or very near the actual rock surface, are similar to those in a *Q. sessiliflora* wood on the Exmoor border (e.g. Horner wood). In some parts where beeches are plentiful the cryptogamic vegetation, on the whole, recalls that seen in the beech-oak woods at Symonds Yat. On Dartmoor the isolated Wistmans Wood and Black Tor Copse consist of the pedunculate oak *Q. robur*, and on the borders, where the woods occupy large areas, this again is the dominant oak, especially on the eastern borders. The woods in the vicinity of Lydford and Okehampton on the north-west borders are dominated mainly by *Q. sessiliflora*. The humid and acidic conditions are more pronounced in the western *Q. sessiliflora* woods, but those of *Q. robur* on the eastern borders are more humid than the *Q. sessiliflora* woods of the Midlands or eastern England. As might be expected, the bryophytic flora, especially the liverworts, is richer in the more humid western woods of *Q. sessiliflora* than in those of *Q. robur* on the eastern borders, though in the latter it is much richer than in an average *Q. robur* wood. Trees of *Q. sessiliflora* or hybrids are occasionally present, and the woods are of a hybrid character in more senses than one. No single factor appears able to determine the dominances of the two oaks; humidity, degree of soil acidity, depth of soil (with which is associated hardness of rock)—all seem to be important. The chief factor determining the occurrence and frequency of bryophytes is humidity. In the *Q. sessiliflora* woods on the west of our islands bryophytes are more frequent than in any other kind of wood, many Atlantic species, especially of hepatics, occurring. These upland woods strewn with boulders and irrigated by numerous streams provide suitable substrata for many of our rarer species. Many localities in Devon, Somerset, north Wales, the Lake District, west Perthshire, Argyllshire or Kerry could be instanced where one or more of the following rare species become abundant in moist or damp situations in *Q. sessiliflora* woods.

### Mosses

*Dieranodontium longirostre*  
*Heterocladium macounii*

*Sematophyllum demissum*  
*S. micans*

### Liverworts

*Adelanthus decipiens*  
*Blepharostoma trichophyllum*  
*Drepanolejeunea hamatifolia*  
*Frullania germana*  
*F. microphylla*

*Harpalejeunea ovata*  
*Herberta hutchinsia*  
*Jamesoniella autumnalis*  
*Jubula hutchinsia*  
*Lejeunea flava*

<sup>1</sup> On the Silurian limestones of the western Midlands the humidity factor is less powerful but *Q. sessiliflora* woods occur (**Salisbury** and **Tansley**, 1921).

*Lejeunea holtii*  
*Lepidozia pinnata*  
*Plagiochila punctata*  
*P. tridenticulata*  
*Ptilidium pulcherrimum*

*Radula aquilegia*  
*R. voluta*  
*Sphenolobus exsectus*  
*S. hellerianus*  
*Trichocolea tomentella*

Humidity is, however, not an unmixed blessing to the lichens. In the humid woods around Killarney the luxuriant growth of *Plagiochila punctata* and other bryophytes on the oaks prevents the occurrence of many lichens, especially crustaceous ones, though these are frequent on the holly where the hepatics are less capable of crowding them out.

In some rocky glens where the water tumbles over the rocks and casts its spray over the surrounding vegetation many lichens exist in the vegetative state only, often only in the powdery sterile conditions known as "leprarioid". In such glens the light intensity is low, and though this does not seriously interfere with the development of woodland bryophytes (in many cases it appears to be beneficial), it certainly does with that of the lichens. Gelatinous lichens may develop luxuriantly, but they are seldom fertile and are usually rare in *Quercus sessiliflora* woods. *Mycoblastus sanguinarius* is one of the few crustaceous lichens which flourishes and "fruits" well under such conditions. Torc Glen, Killarney, and Launchy Gill, Thirlmere, supply extreme examples of woods with such spray-laden atmospheres that liverworts thrive and lichens almost disappear. Other well-known examples are the woods near the famous waterfall, Rhaidr Du, at Tyn-y-Groes and those in Lydford Gorge. At Launchy Gill *Herberta hutchinsia* and *Anastrepta orcadensis* are frequent, near Rhaidr Du *Leptodontium recurvifolium* occurs and *Jamesoniella autumnalis* and *Dicranodontium longirostre* are abundant, in Lydford Gorge *Jubula hutchinsia* forms a green mantle on the damp rocky ledges, whilst Torc Cascade is famous for the wealth of its hepatics. Three examples of such rocky glens, two of which are in *Quercus sessiliflora* woods, are given in "The bryophytes and lichens of fresh water" (Watson, 1919), with a comparative list of the bryophytes found in them.

#### PEDUNCULATE OAK WOODS

In the previous pages some references have been made to *Q. robur* woods: their bryophytes (and lichens in part) have been previously dealt with by Watson (1909) as oak-hazel, and by Salisbury (1925), oak-hornbeam (1916, 1918), and comparisons with other woods can be made from the general lists.

Salisbury (1916, 1918) in his account of the oak-hornbeam woods of Hertfordshire, gave a list of the bryophytes and, in part, of the lichens. When allowance is made for the eastern position of the woods, the lists, taken generally, do not differ much from those in which oak is the only dominant. From the lists it seems as if some species from the beechwood had been added to those from the oak wood.<sup>1</sup> This is not surprising when we remember that

<sup>1</sup> This applies to both kinds of oak-hornbeam woods, those in which *Q. sessiliflora* is present and those with *Q. robur*.

these hornbeam woods are situated in the same climatic region as the typical south-eastern beech woods, and that the barks of the hornbeam and beech are similar in regard to epiphytic growth. We should rather expect the lichens and bryophytes to be similar when other conditions are equal. In a rather mixed wood near Crowcombe, Somerset, planted beech is dominant in one portion. In an adjoining area planted hornbeams are frequent and their epiphytic mantle is similar to that of the beeches. *Eurhynchium myosuroides*, *Hypnum cupressiforme*, *Metzgeria furcata* and *Neckera pumila* were the commonest bryophytes. The lichens in this area common to the two kinds of tree were:

<i>Acrocordia biformis</i>	o.	<i>Lecidea parasema</i> and var. <i>flavens</i>	a.
<i>Enterographa crassa</i>	a.	<i>Parmelia fuliginosa</i> var. <i>lactevirens</i>	r.
<i>Graphis elegans</i>	r.	<i>P. tiliacea</i>	r.
<i>G. scripta</i>	a.	<i>Portusaria amara</i>	o.
<i>Lecanora chlaronia</i>	f.	<i>P. communis</i>	o.
<i>L. intumescens</i>	r.	<i>P. leioplaca</i>	o.
<i>L. glabrata</i>	r.	<i>Phlyctis agelaea</i>	o.

As the wood also contained oak (f.), pine (o.), ash (o.), birch (o.), elder (o.), sycamore (o.), mountain ash (o.), the comparison of the ground floras in the beech and hornbeam portions would have been of little value. The corticicolous species in the oak-hornbeam woods of Hertfordshire are similar to those of the oak-beech woods at Symonds Yat, but the ground flora is very different.

#### OAK-BEECH WOODS

Armitage (1914) gave a list of the bryophytes in the oak-beech woods on the Carboniferous limestone of the Wye Gorge at Symonds Yat. Both species of oak are present, *Quercus robur* being more abundant than *Q. sessiliflora*, though the latter is now probably less common than it formerly was. The list given in column 11 follows after that mentioned above, with the addition of plants (chiefly lichens) noted during an investigation of the wood when the British Bryological Society held some field days in the district. The general flora is akin to that of an oak wood, but the bryophytes and lichens of the more or less open and rocky places in the wood correspond more to those of ash scrub.

The woods by the side of the Lower Lake in the Muckcross demesne at Killarney are also on the same substratum. The oak is *Q. sessiliflora* and in parts planted beech is co-dominant. These portions, except for some plants which are local or are consequent on the more humid and milder climate, are comparable with those of Symonds Yat. The epilithic flora is almost identical and the bryophytes and lichens of the ground are very similar. The corticicolous mantle shows many plants which are frequent in the oakwoods of the Killarney district but rare or absent at Symonds Yat. The following plants (some of which are not corticicolous) which are absent or rare in the Wye Gorge were frequent at Muckcross.

*Mosses*

*Eurhynchium circinatum*  
*Hyocomium flagellare*  
*Orthotrichum leiocarpum*

*Ulota phyllantha* (abundant as in all  
 parts of Kerry)

*Liverworts*

*Bazzania trilobata*  
*Plagiochila punctata*  
*P. spinulosa*

*Radula carringtonii*  
*Saccogyna viticulosa*

*Lichens*

*Arthopyrenia saxicola*  
*A. stigmatella*  
*Collema granosum*  
*Leptogium plicatilo*  
*L. sinuatum*  
*Lobaria laetevirens* a.  
*L. pulmonaria* a.

*Microthelia micula*  
*Pannaria rubiginosa* a.  
*Parmeliella atlantica* a.  
*P. plumbea* a.  
*Stictina fuliginosa* a.  
*S. silvatica*  
*Thelotrema lepadinum*

## HEATHY OAK WOODS

In the heathy oak woods many bryophytes and lichens which are more frequent on heaths occur and the list could be extended so as to include a number of other heath plants which are more or less incidental to the woodland area. In consequence of this the absence of a frequency indicator for a particular species may not imply that it is always absent. As might be expected, the flora is variable, but generally speaking the bryophytic flora is poorer and the lichen ground flora richer than in an oakwood in the same district. In one wood on the Pennines which was investigated the flora was poor and true woodland species were few in number. Oak was the most abundant tree but birch, pine, larch, mountain ash, and holly were also present, with patches of ling, heather, whortleberry, *Molinia*, *Deschampsia*, *Juncus* and bracken. The chief bryophytes and lichens were:

*Mosses*

*Atrichum undulatum*  
*Ceratodon purpureus*  
*Dicranella heteromalla*  
*Orthodontium heterocarpum*  
*Polytrichum aloides*

*Polytrichum formosum*  
*Plagiothecium elegans*  
*Tetraphis pellucida*  
*Webera nutans*

*Liverworts*

*Calypogeia fissa*  
*C. trichomanis*

*Lepidozia reptans*  
*Lophozia floerkii*

*Lichens*

*Cladonia coccifera*  
*C. pyxidata*  
*C. subcervicornis*

*Lecanora conizaeoides*  
*L. polytropa*  
*Lecideia granulosa*

together with *Bryum pseudotriquetrum*, *Lepidozia setacea*, *Mnium punctatum*, *Scapania dentata* and *S. undulata* in wetter places.

Some degenerate woods of this kind are mentioned in the "Bryophytes and lichens of Moorland" (Watson, 1932) in connection with the wet heaths of Skipwith and Lindow Common, and a list of the bryophytes and lichens on the latter is given.

When an oak wood degenerates into heathy woodland many species of heath plants appear, especially *Campylopus pyriformis*, *Webera nutans*, *Calypogeia trichomanis*, *Ptilidium ciliare*, *Baeomyces rufus*, *Cladina sylvatica*, *Cladonia coccifera*, *C. crispata*, *Biatora granulosa* and *B. uliginosa*, but even in open places some of the shade plants may remain for some time. Conversely when the wood originates on heath the typical heath plants tend to disappear. They may remain for many years in open places, but in the more shaded portions they gradually disappear. When bracken becomes abundant in the wood, many bryophytes and lichens are eliminated, though *Brachythecium purum*, *Hypnum cupressiforme* var. *ericetorum*, *H. schreberi*, *Hylocomium splendens* and *Ptilidium ciliare* may still remain or become more frequent. The invasion by gorse also has a smothering effect. When the species is *Ulex europaeus* later stages become less exclusive for the ground carpet and, on the older stems, bryophytes such as *Microlejeunea ulicina* and *Cololejeunea minutissima*, and lichens such as species of *Lecanora* may occur.

#### OAK-BIRCH WOODS

There are some woods which naturally fall under this category, but no sharp line can be drawn between them and heathy oak woods. Most oak-birch woods become heathy in places and most heathy oak woods contain birch. A preliminary or trial list was made of species found in oak-birch woods and this showed that most of the species were common to oak and birch woods, but had slightly different frequency values which were nearer those of the birch woods than those of the oak woods. Bryophytes characteristic of heaths became more abundant but the general bryophytic flora was poorer than that of an oak wood in the same district.

#### OAK WOODS WITH PLANTED CONIFERS

In these there is also a tendency to approximate to heathy oak woods. A preliminary trial list showed that the flora was nearer to that of the oak wood than of a coniferous one. The ground flora was not so rich as in an oak wood, many plants being less frequent or absent, but the frequency of some plants was increased. There is a tendency for such bryophytes as the following to become more frequent, and when conifers are felled some of them are reduced or may even be eliminated.

#### Mosses

*Aulacomnium androgynum*  
*Brachythecium purum*  
*Buxbaumia aphylla*  
*B. indusiata*  
*Campylopus fragilis*  
*C. pyriformis*  
*Dicranum undulatum*  
*Hylocomium loreum*  
*H. squarrosum*  
*H. triquetrum*

*Hypnum cristacastrensis*  
*Leucobryum glaucum*  
*Plagiothecium undulatum*  
*Polytrichum aloides*  
*P. commune*  
*P. formosum*  
*P. gracile*  
*P. juniperinum*  
*P. piliferum*  
*Tetraphis pellucida*



*Liverworts*

*Alicularia scalaris*  
*Calypogeia trichomanis*  
*Diplophyllum albicans*  
*Lepidozia reptans*  
*Lophozia ventricosa*

*Ptilidium ciliare*  
*Scapania compacta*  
*S. gracilis*  
*S. umbrosa*

Among the terricolous or saxicolous lichens *Baeomyces roseus*, *B. rufus*, *Botrydina vulgaris* and *Cladina sylvatica* tend to become more abundant. The corticolous lichens mentioned on p. 477 as showing a preference for conifers are more frequent, while those specified as not usually found on conifers are rarer or absent.

## BIRCH WOODS. CONIFEROUS WOODS

The list flatters both birch and coniferous woods. It gives, as for the other woods, the different species present and their frequencies, but on examining a particular birch or a particular coniferous wood there would be more absentee members than if a particular oak or ash wood had been examined. Again the frequency indicators have not exactly the same value. The "occasional" species occur more rarely. If one expressed "occasional" by the figure 2 and "rare" by 1, most of the "occasionals" for birch or coniferous wood would be marked between 1.5 and 2, whereas in oak or ash woods they would mostly lie between 2 and 2.5. Epiphytic vegetation on both the birches and the conifers is poor, possibly because of the continual peeling of the bark. On the loosened bark of the birch undeveloped perithecia of lichens are not uncommon, though this must not be taken to imply that pyrenocarpous lichens are unable to form, since some (e.g. *Arthopyrenia*, *Leptorhaphis*) have certainly sufficient time and opportunity to do so.

No discrimination was made between the different kinds of birch.

The coniferous woods are much alike in regard to the species occurring on the trees. When the woods are dense both bryophytes and lichens are often absent whilst those on the ground are few in number, partly owing to the dense shade, but largely because of the slow decay of the leaf litter. Even when the trees are larch, terricolous species are less evident than would be expected considering the deciduous nature of the trees. In a particular dense coniferous wood (pine and larch) examined, the trunks of the trees were devoid of bryophytes or foliaceous lichens, though these were present on some angiospermous trees further in the wood. A few crustaceous lichens were present; *Lecanora expallens* often more or less leprarioid, *Biatorina griffithii* on larches, and *Opegrapha vulgata* on pines. On the ground *Brachythecium rutabulum* often occurred, especially at the bases of trees; *Eurhynchium praelongum* on the soil or on pine cones and *Fissidens bryoides* were occasional. In a spruce plantation *Lecanora expallens* was again the most abundant lichen, but the ground carpet was almost entirely composed of *Brachythecium purum* and *Nepeta glechoma* with *Hylocomium squarrosum* and *Atrichum undulatum* fre-

quent on grassy patches in less shaded places. *Lophocolea heterophylla* occurred on stumps, whilst *Dicranella heteromalla* and *Pleuridium subulatum* were noted in more open places.

The list is not made from coniferous plantations in which the light intensity is low, though their contents have been taken into account during its preparation. The list is fairly average for a subspontaneous or a natural pine wood, in both of which the light intensity is generally higher than in a plantation of conifers. If the natural wood and the subspontaneous one were in the same district the bryophytes and lichens would be fairly conformable, but, as the former are chiefly in Scotland and the latter chiefly in south-east England, some adjustment will usually be necessary on account of differences in the geographical distribution of the species.

In some of the natural pine woods of Scotland there is a slight preference shown by some species of *Sphagnum* which are not truly woodland species and are not given in the general list. When *Sphagnum fimbriatum*, *S. fuscum*, *S. girgensohnii*, *S. imbricatum*, *S. medium*, *S. russowii* and *S. warnstorffii* are present in woods, conifers and/or birches are usually present.

In some pine woods at Seatoller and Buttermere, undoubtedly planted but with a fairly natural appearance, where the pines were more openly spaced, the ground flora and the lichens on the tree trunks were richer. Besides the usual patches of *Parmelia* and *Evernia* the following occurred:

Allarthonia patellulata	Parmeliopsis ambigua
Biatora viridescens	P. hyperopta
Biatorina atropurpurea	Stictina fuliginosa
B. erysiboides	S. limbata
Lecania dubitans	Toninia canadensis
Microphiale diluta	

Most of these are more frequently found on conifers than on angiosperms, *Biatora erysiboides* and *Microphiale diluta* being more often at the base of the trunk than in any other situation.

#### ASH WOOD AND ASH SCRUB

An account of ash woods is given in an earlier paper (Watson, 1909). They are usually over limestone and, from a bryophytic standpoint, are often dominated by *Hypnum molluscum*. The following are frequent or characteristic species.

#### Mosses

Amblystegium confervoides r.	Dicranum scoparium
Anomodon longifolius r.	Ditrichum flexicaule
A. viticulosus	Encalypta streptocarpa
Barbula cylindrica	Eurhynchium crassinervium
B. fallax	E. praelongum
Brachythecium rutabulum	E. striatum (often s.d.)
Bryum capillare	E. tenellum
B. provinciale r.	Fissidens adiantoides (dry ground form)
Camptothecium sericeum	F. decipiens
Campylium chrysophyllum	F. viridulus
C. hispidulum var. sommerfeltii r.	Hylocomium brevirostre

*Hylocomium triquetrum*  
*Hypnum cupressiforme*  
*H. cuspidatum* (dry ground form)  
*Mnium affine*  
*M. cuspidatum*  
*M. rostratum*  
*M. stellare*  
*M. undulatum*  
*Neckera complanata*

*Neckera crispa*  
*N. pumila*  
*Plagiothecium denticulatum*  
*P. sylvaticum*  
*Porotrichum alopecurum*  
*Seligeria pusilla*  
*Thuidium philiberti*  
*T. tamariscinum*  
*Trichostomum tortuosum*

*Liverworts*

*Frullania dilatata*  
*F. tamarisci*  
*Lejeunea cavifolia*  
*Lophocolea cuspidata*  
*L. heterophylla*  
*Madotheca platyphylla*

*Marchesinia mackaii*  
*Metzgeria furcata*  
*Plagiochila asplenioides*  
*Reboulia hemispherica*  
*Scapania aspera*

## In wetter places appear:

*Amblystegium filicinum*  
*Drepanocladus commutatus*  
*Eurhynchium rusciforme*  
*E. tcecdalei* (r.)  
*Mnium punctatum*

*Weisia verticillata*  
*Lophozia badensis*  
*L. turbinata*  
*Pellia fabbronia*  
*Preissia quadrata*

*Lichens*

Among lichens the following are characteristic but not always frequent:

*Biatorina lenticularis*  
*Bilimbia albidocarpa* r.  
*Cladonia pyxidata* var. *pocilla*  
*C. rangiformis*  
*Clathroporina calcarca* r.  
*Collema pulposum*  
*Dermatocarpon lachneum*  
*D. miniatum*  
*Gyalecta carneolutea* r.  
*G. cupularis*  
*Leptogium lacerum*  
*Opegrapha atra*

*Opegrapha vulgata*  
*Peltigera polydaetyla* and other spp.  
*Petractis clausa*  
*Physcia hispida*  
*P. elacina*  
*P. pulverulenta*  
*Pyrenula nitida*  
*Ramalina calicaris*  
*R. fastigiata*  
*R. fraxinea*  
*Solorina saccata*

The main difficulty in drawing up the list was in regard to the boundary between wood and scrub. A number of plants which are frequent in the scrub are also listed for the wood. In an ash wood with little or no exposed rock these species become rare or are absent, but where the rock surface is more exposed they become more frequent and even some of the species given for scrub only may occur.

The scrub contains many species which are partial to the soil caps or nooks or crannies or surfaces of limestone rock.

*Mosses*

*Bryum caespiticium*  
*B. inclinatum*  
*B. pendulum*  
*Camptothecium lutescens*  
*C. sericeum*  
*Encalypta streptocarpa*  
*E. vulgaris*  
*Eurhynchium circinatum*  
*E. murale*  
*E. striatulum*  
*E. swartzii*  
*E. tenellum*  
*Funaria calcarca*

*Grimmia apocarpa*  
*G. orbicularis*  
*G. pulvinata*  
*Hypnum molluscum*  
*Neckera crispa*  
*Orthotrichum anomalum* var. *saxatile*  
*Pleurochaete squarrosa*  
*Seligeria pusilla*  
*Tortula intermedia*  
*T. muralis*  
*T. subulata*  
*Trichostomum crispulum*  
*T. nitidum*

*Liverworts*

Cololejeunea rossettiana  
 Lophocolea cuspidata  
 Lunularia cruciata  
 Marchesia mackaii  
 Pedinophyllum interruptum

Reboulia hemisphaerica  
 Scapania aequiloba  
 S. curta  
 S. cuspiduligera  
 S. nemorosa

*Lichens*

Acrocordia epipolia  
 Arthopyrenia saxicola  
 Aspicilia calcarea  
 A. prevostii  
 Biatora fusciorubens  
 Biatorina lenticularis  
 Bilimbia albidocarpa  
 Buellia myriocarpa  
 Callopisma citrina  
 Cladonia pyxidata var. pocilla  
 Clathroporina calcarea  
 Collema crispum  
 C. furvum  
 C. granosum  
 C. granuliferum  
 C. multifidum  
 C. pulposum  
 C. tenax  
 Dermatocarpon hepaticum  
 D. lachneum  
 D. miniatum  
 Diploicia canescens  
 Diploschistes gypsaceus  
 D. scruposus  
 Lecania erysibe  
 Lecidea jurana  
 Physcia aipolia

Physcia grisea  
 P. pulverulenta  
 P. virella  
 Placodium callopismum var. plicatum  
 P. murorum  
 P. cirrochroum  
 P. xantholytum  
 Placynthium nigrum  
 Porina chlorotica var. linearis  
 Psora lurida  
 Rhizocarpon alboatrum  
 Staurothole cbborensis  
 S. rupifraga  
 Synechoblastus rupestris  
 S. multipartitus  
 S. laureri  
 Thalloidima candidum  
 T. coeruleonigricans  
 Thelidium immersum  
 T. incavatum  
 Toninia aromatica  
 Verrucaria integra  
 V. muralis  
 V. parva  
 V. rupestris  
 V. sphinctrina

It is in the scrub that protective devices (Watson, 1914) for the bryophytes are best shown.

Involution (*Trichostomum crispulum*) or revolution of leaf margin (*Tortula muralis*), undulation or plication of leaf surface (*Eurhynchium striatulum*), hair points (*T. muralis*, *Grimmia pulvinata*), hyaline or thickened borders (*T. muralis*, *G. orbicularis*), imbrication (*Tortula intermedia*, *Bryum pendulum*) or twisting of leaves or shoots (*Eurhynchium circinatum*), tufted habit (*Grimmia pulvinata*, *Tortula muralis*, *Trichostomum nitidum*, *Encalypta vulgaris*), water chambers (*Marchesia*), and many other devices for preventing undue evaporation or for conservation of water, are shown by some of the scrub plants.

The commonest bryophytes of the actual ash wood are usually little different from an average moss or liverwort. Most corticicolous bryophytes show some slight adaptation for retaining or storing water: in the liverworts there is often some kind of space which acts as a water-sac. They are well shown in members of Lejeuneaceae and of the genera *Frullania*, *Radula*, *Madothea*, which include the greater number of our frequent corticicolous liverworts. The undulations of the leaves in some shade plants may be useful in giving a greater leaf surface for light absorption, but the foldings are often useful for decreasing evaporation of water. In some plants such as *Mnium undulatum* the undulations tend to disappear when they grow under wetter conditions.

## ALDER WOODS

In these the ground is often swampy, willows sometimes compete for dominance and occasional birches usually occur. The ground carpet of bryophytes is not rich. *Climacium dendroides*, *Hypnum cuspidatum*, *H. cordifolium*, *H. giganteum*, *Brachythecium purum* and *Campylium riparium*, being characteristic species. Hepatics are not common, though *Pellia epiphylla* and species of *Cephalozia* (*C. bicuspidata*, *C. connivens*, etc.) are sometimes frequent. On the alder epiphytic vegetation is not common, the most widely distributed and frequent being:

*Eurhynchium myosuroides*  
*E. myurum*  
*Hypnum cupressiforme*

*Frullania dilatata*  
*Metzgeria furcata*

*Arthonia radiata*  
*Arthopyrenia punctiformis*  
*Evernia prunastri*  
*Lecanora chloroneura*  
*Lecidea parasema*  
*Ramalina farinacea*  
*R. fastigiata*

*Stenocybe byssacea* seems to be peculiar to the alder but is often absent from those growing in an alder swamp, preferring the trees near running water.

*Sphagna* are usually absent but not invariably. In some alder woods they occur and in a few instances their species have been determined. In the carr surrounding Esthwaite Water alder is abundant and with it *S. amblyphyllum* and *S. inundatum* occur. At Cannock Chase *S. cymbifolium*, *S. acutifolium* and *S. recurvum* were noted. On Chard Common *S. papillosum*, *S. cymbifolium* var. *squarrosulum*, *S. recurvum*, *S. rubellum*, *S. subsecundum* and *S. inundatum* were observed. In an alder and willow swamp with an occasional tree of *Quercus sessiliflora*, near Eagle's Nest, Killarney, forms of *S. recurvum* occur, and on the wet heathy places at Skipwith, Studland and Shapwick *Sphagna* occur under or near alders and willows.

## SPHAGNUM IN WOODS

Species of *Sphagnum* are sometimes found in the wetter parts of woods, especially in those of *Quercus sessiliflora*. *Sphagnum quinquefarium* and *S. squarrosum* are often present, but other species such as *S. acutifolium*, *S. amblyphyllum*, *S. auriculatum*, *S. cymbifolium*, *S. inundatum*, *S. molle*, *S. papillosum*, *S. plumulosum*, *S. subsecundum*, and *S. turgidulum* occasionally occur when light and humidity conditions are favourable.

*S. quinquefarium* has a definite right to be included in the list as a woodland species. It often occurs in large pure masses on wooded slopes far above the stream-level and in much drier situations than other species. *S. squarrosum* also has some claim to be considered as truly woodland and some of the squarrose-leaved varieties of other species (e.g. *S. cymbifolium* var. *squarrosulum*, *S. compactum* var. *squarrosum*) are more prevalent in woods than their types. *S. compactum* is a heath plant, but it occasionally occurs in heathy woods, and its variety *squarrosum* is recorded by Richards (1928) for oak-

hornbeam woods. In the wet parts of heathy oakwoods *S. amblyphyllum*, *S. auriculatum*, *S. compactum*, *S. cymbifolium*, *S. papillosum*, *S. recurvum* and other species occur. *Sphagnum* is seldom present in *Quercus robur* or ash-oak woods, though *Sphagnum recurvum* has sometimes been met with in quantity in ditches by the sides of "rides". In the wetter parts of birch and coniferous woods *Sphagna* are sometimes more frequent than in *Quercus sessiliflora* woods. Many species occur and the following appear to be more frequent in such woods than in any other:

*Sphagnum fimbriatum*  
*S. fuscum*  
*S. girgensohnii*  
*S. imbricatum*

*Sphagnum medium*  
*S. rubellum*  
*S. russowii*  
*S. warnstofi*

Alder woods are often considered unsuitable for *Sphagna*, but some species may occur (see p. 474).

Ash and beech woods are normally free from *Sphagna*, but species occasionally occur in some of the acidic beech woods around London.

#### CORTICICOLOUS BRYOPHYTES AND LICHENS

As a general rule the bryophytes are more abundant on or towards that side of the tree where most rain falls, whilst lichens, especially crustaceous ones, are on or towards the other side. In Somerset, where the rainy winds usually come from a south or western direction, the bryophytes are on the west and south sides of oak trunks whilst the crustaceous lichens are on the east side, though local currents sometimes modify this arrangement. The soil has very little direct influence on these epiphytes. Particles of dust may be driven by the wind against the trunk and so provide some nutriment which can be dissolved in the water when it is present on the trunk. In this way some slight differentiation may exist between the corticicolous species on two distinct substrata, and a certain differential action of this kind has actually been observed in a calcareous district. The soil, however, is an important factor in determining what kinds of trees are present, so that there would be an indirect influence of the soil on the epiphytes if there is a specific ecological relationship between the epiphytes and the tree on which it grows.

The chief factors influencing the lichens and bryophytes on tree trunks are (1) the character of the surface, (2) the degree of humidity, (3) the light intensity, (4) the temperature, and (5) the purity of the air.

The birches and the conifers have the fewest epiphytes and this is probably because of their peeling barks (see p. 470). The trees with smooth bark have fewer epiphytes than those with rougher bark. Bryophytes are few on smooth bark, though some closely applied plants such as *Neckera pumila*, *Radula Metzgeria*, *Frullania*, *Microlejeunea* and other members of *Lejeuneaceae* are not uncommon and crustaceous lichens are often found. Most mosses and the foliose or fruticose lichens require some roughness before they develop. As this character varies with age in most trees the lichens which are present on

the trunks of the young trees, or on the smoother bark of branches of the older trees are often different from those on the trunks of the older trees. On young oaks, when the bark of the main trunk is smooth, crustaceous lichens with little or no superficial thallus occur, such as:

<i>Acrocordia biformis</i>	<i>Arthopyrenia fallax</i>
<i>A. gemmata</i>	<i>A. punctiformis</i>
<i>Arthopyrenia analepta</i>	<i>A. stigmatella</i>
<i>A. cineropruinosa</i>	<i>Graphis scripta</i>
<i>A. epidermidis</i>	<i>Opegrapha vulgata</i>

The trunks and main branches of older oaks are clothed with species of *Evernia*, *Parmelia*, *Platysma*, *Ramalina*, *Usnea*, etc. Many of the crustaceous lichens, frequent when the oaks were young, have completely disappeared, though some with definite epiphloedal thalli, such as *Lecidea parasema*, *Lecanora* species, *Lecanactis abietina*, *Enterographa crassa*, *Pertusaria amara*, *P. communis*, *P. wulfenii* and *Phlyctis* become more frequent and even abundant. Elms and poplars also show noticeable differences between the epiphytes on old and young trees, the species concerned being different from those mentioned for the oak, though this difference does not necessarily entail direct biotic relationship.

Humidity is much more necessary for most bryophytes, especially hepatics, than for most lichens. Many bryophytes become more luxuriant and may even exhibit structural changes with increasing humidity. Many epiphytes (both bryophytes and lichens) which usually occur only at the base of the tree may extend some distance up the trunk, e.g.

<i>Atrichum undulatum</i>	<i>Lepidozia reptans</i>
<i>Campylopus fragilis</i>	<i>Plagiochila asplenoides</i>
<i>Eurhynchium myosuroides</i>	
<i>E. myurum</i>	<i>Biatora micrococca</i>
<i>Leucobryum glaucum</i>	<i>Biatorina erysibides</i>
<i>Mnium hornum</i>	<i>Microphiale diluta</i>
<i>Plagiothecium silvaticum</i>	<i>Porina leptalea</i>
<i>Thuidium tamariscinum</i>	<i>Sphaerophorus corallioides</i>

Some other effects are mentioned on previous pages (pp. 466, 470).

Many bryophytes are capable of normal growth under varying conditions of illumination, but others become "drawn" when the light intensity is low, the leaves being more scattered and smaller. Some pleurocarpous mosses, such as *Eurhynchium praelongum*, may even lose their characteristic pinnation. Lichens are usually more susceptible to changes in light intensity, and in deep shade may exist merely in a leprarioid conditions. *Evernia prunastri* seems to be more tolerant of shade than species of *Usnea* or *Ramalina*.

Most of these plants can endure a wide range of temperature, but some have a northern and some a southern distribution (see p. 449-450), apparently on account of different adjustments to temperature.

The purity of the air is important for both bryophytes and lichens, though the latter show on the whole the greatest susceptibility in this respect.

Some bryophytes and lichens seem to show a preference for certain trees where, *under average conditions*, the factors determining their occurrence are

apparently at their optima. An attachment to the elder is shown by more plants than *Hirneola*; *Cryphaea heteromalla*, *Callopisma cerinellum* and *Lecanora sambuci* have a distinct preference for the elder, whilst species of *Orthotrichum*, *Ulota*, *Bacidia*, *Lecania* and *Xanthoria* are often frequent on this shrub. In very damp situations, however, some of these disappear, so that the qualification "under average conditions" is necessary. *Stenocybe byssacea* is nearly always found on alder branches overhanging a stream, and some other lichens (e.g. *Arthopyrenia punctiformis*) are frequent on the trunks. The bark of the oak trunk is the special home of such lichens as:

*Arthonia pruinata*  
*Lecanactis abietina*  
*L. premnea*  
*Lobaria laetevirens*

*Pannaria rubiginosa*  
*Parmeliella plumbea*  
*P. atlantica*  
*Rinodina roboris*

The holly is usually poor in epiphytic bryophytes and the larger lichens, but it offers a suitable substratum for such crustaceous lichens as the species belonging to the Graphidales and Pyrenocarpales. *Thelotrema* is often found on the holly and *Stenocybe septata* has a decided preference for it. Ash, elm, sycamore and poplar are often rich both in bryophytes and lichens, and a number of species more or less preferring each could be noted. On the birch the epiphytic covering is poor and very diffuse, but *Leptorhaphis epidermidis* and *Cetraria cucullata* are seldom found on other trees. The conifers do not display an epiphytic mantle. Such bryophytes as *Eurhynchium praelongum*, *Frullania dilatata*, *Hypnum cupressiforme*, *Lophocolea*, *Microlejeunea*, *Thuidium tamariscinum* do occur towards the bases but they rarely run up the trunks. The rare *Buxbaumia indusiata* may be found at the bases of conifers but species of *Ulota* and *Orthotrichum*, common on so many trees, seldom occur. In the humid districts around Dingle, Ventry and Killarney, luxuriant *Ulota phyllantha* seems to be abundant on all trees except holly, birch and conifers. The most frequent lichens (such as *Evernia prunastri*) on conifers also occur on broad-leaved trees, but some lichens seem to have a distinct preference for the former while others which are found on the latter are rarer (sometimes absent) on conifers.

The following show a preference for conifers:

*Alectoria yubata*  
*Biatra micrococca*  
*B. mutabilis*  
*B. viridescens*  
*Biatorella pinicola*  
*Biatorina chlorococca*  
*B. erysiboides*  
*B. spodiza*  
*Chaenotheca chrysocephala*  
*C. melanophaca*

*Lecanora piniperda*  
*Mencgazzia pertusa* (also birch)  
*Microphiale diluta*  
*Ochrolechia tartarea*  
*Parmeliopsis ambigua*  
*P. hyperopta*  
*Platysma pinastri*  
*Porina leptalea*  
*Psora ostryea*  
*Tomnia caradocensis*

*Allarthonia patellulata* and *Lecania dubitans*, which Arnold (1900) says do not occur on conifers at Munich, seem with us to be more abundant at the bases of conifers than elsewhere.



The following are not (or rarely) present on conifers:

Acrocordia gemmata	Lobaria scrobiculata
Arthonia punctiformis	Mycoporum quercus
Arthopyrenia fallax	Opegrapha atra
A. laburni	O. betulina
A. punctiformis	Parmelia acetabulum
A. stigmatella	P. dubia
Bacidia atrogrisea	P. exasperata
B. beckhausii	Peltigera spp
B. luteola	Pertusaria communis
Biatorina graniformis	P. globulifera
B. globulosa	P. leioplaca
Bilimbia sabuletorum	Phlyctis agelaea
Callopisma cerinum	Physcia aipolia
C. phloginum	P. claeina
Candelaria concolor	P. hispida
Gyalecta flotovii	P. pulverulenta
Lecania syringea	P. virella
Lecanora intumescens	Ramalina fraxinea
Leptogium spp	Rhizocarpon alboatrum
Leptorhaphis epidermidis	Rinodina sophodes
L. carrollii	Sphinctrina turbinata
Lobaria pulmonaria	Stenocybe byssacea

#### REFERENCES

These are as in Part I (p. 160) with the following additions:

- Arnold, F.** "Zur Lichenflora von München." München 1891-1901,  
**Horwood, A. H.** "The cryptogamic flora of Leicestershire." *Trans. Leices. Lit. Phil. Soc.* 1909.  
**Watson, W.** "Lichenological notes. VII." *J. Bot.* 1933.  
**Watson, W.** "The bryophytes and lichens of Moorland." *This JOURN.* **20**, 1932.  
**Watt, A. S.** "The vegetation of the Chiltern Hills." *This JOURN.* **22**, 1934.

# THE WEED SEED POPULATION OF ARABLE SOIL

## III. THE RE-ESTABLISHMENT OF WEED SPECIES AFTER REDUCTION BY FALLOWING

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*(With eight Figures in the Text)*

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### I. INTRODUCTION

FROM the practical point of view the most important feature of weed reduction by various methods of treatment is the length of time that such reduction remains effective. Special methods of eradication involve extra expense, and, if fallowing is carried out, loss of crops as well. If pernicious weeds can be drastically reduced by such methods, the expense and trouble involved is justified from an economic point of view provided the number of such weeds remains at a low level for several succeeding years. If, however, the weeds re-establish themselves very rapidly it is probable that the increased crop resulting from the temporary reduction of competition will not compensate for the extra outlay. Hitherto practically no quantitative information has been available as to the behaviour of weeds after such drastic methods of reduction as fallowing. Most cultivators have their own ideas on the subject, and divergent opinions are held owing to differences in local conditions and the varying quality of the observations made.

For the past eleven years, since autumn 1925, a continuous quantitative experiment has been carried out on Broadbalk wheat field at Rothamsted, in which the potential weed flora has been estimated by recording the weed seedlings obtained from numerous soil samples taken year after year from the same areas immediately after harvest. During the first four years all parts of the field were subjected to either two or four years' consecutive fallow, the whole area returning into crop in the autumn of 1929. In addition to the fallowing, special attention was devoted to the eradication of weeds among the crop, in the hope of effecting a real reduction by a combination of the two methods of control. Two previous papers have demonstrated the enormous potential weed flora, as indicated by the number of living seeds present in the soil before active measures were taken, and the comparative effect of fallowing and cultivation among the crop on the numbers of these viable seeds (Brenchley and Warington, 1930, 1933). In nearly every case adequate fallowing caused a more or less considerable decrease in the potential flora, but the effects of crop cultivation varied widely, from a decrease equal to that caused by fallowing to an increase to two or three times the original number.

The methods used in obtaining the seedlings and in handling the large numbers of figures entailed were fully described in the first paper (Brenchley and Warington, 1930, pp. 238-41), to which reference should be made. Data are now available showing the after-effects of fallowing for varying periods, when the land has again been cropped for several successive seasons, but before these can be dealt with profitably, certain other points need discussion.

## II. EFFECT OF TIME OF FALLOWING ON THE WEED FLORA

Early ploughing of the stubble encourages germination, and many of these seedlings are probably killed by winter conditions, while the great majority of the remainder are cut down by spring cultivations before they flower and ripen seeds. This is true for all except a very few species, notably *Capsella bursa-pastoris*, *Arenaria serpyllifolia*, *Veronica buxbaumii* and *Poa annua*, which are able to reach the seeding stage very rapidly even in the autumn and winter months, and so can maintain their numbers of seeds in the soil in spite of repeated later cultivations.

Under normal conditions fallowing operations begin by cultivating or ploughing the stubble as soon as possible after harvest. When the time arrived to begin the fallowing of the second half of Broadbalk field, the area was left untouched, owing to unavoidable circumstances, from harvest in August 1927 till March 1928. The first ploughing was then done, and fallowing operations carried on in the normal way. The delay in ploughing influenced the behaviour of various species in different ways, so that in some cases the results of the first year under fallow do not correspond with those obtained previously during the parallel period on the other part of the field.

When the autumn stubble ploughing was omitted in 1927, an opportunity was provided for several weed species to increase their stocks of seed in the soil (Table I). Weeds were plentiful in the stubble, and many of them doubtless

Table I. *Number of viable buried seeds in successive years (all seven plots together)*

Land cropped 1927; fallowed 1928, 1929; cropped 1930.

	Actual population per 14 sq. ft.				Relative population in percentages			
	1927	1928	1929	1930	1927	1928	1929	1930
Grass, chiefly <i>Poa annua</i>	22	171	49	139	100	777	223	632
<i>Bartsia odontites</i>	20	62	37	131	100	310	185	655
<i>Capsella bursa-pastoris</i>	307	893	380	561	100	290	124	183
<i>Senecio vulgaris</i>	96	148	34	19	100	154	35	20
<i>Arenaria serpyllifolia</i>	269	406	211	333	100	151	78	124
<i>Atriplex patula</i>	124	186	15	34	100	150	12	27
<i>Stellaria media</i>	29	42	31	78	100	145	107	269
<i>Matricaria inodora</i>	20	28	16	28	100	140	80	140
<i>Polygonum aviculare</i>	44	55	15	32	100	125	34	73
<i>Veronica hederæfolia</i>	296	345	134	246	100	117	45	83
<i>V. buxbaumii</i>	361	404	130	77	100	112	36	21
<i>Euphorbia exigua</i>	21	23	6	18	100	110	29	86
<i>Anagallis arvensis</i>	24	26	17	11	100	108	71	46
<i>Legousia hybrida</i>	168	168	98	284	100	100	58	169
<i>Linaria minor</i>	55	51	46	23	100	93	84	42
<i>Scandix pecten</i>	16	14	1	9	100	88	6	56
<i>Caucalis arvensis</i>	80	65	46	49	100	81	58	61
<i>Polygonum convolvulus</i>	9	7	1	2	100	78	11	22
<i>Papaver</i> spp.	39,078	29,037	17,407	23,031	100	74	45	59
<i>Veronica arvensis</i>	1,204	867	522	1,484	100	72	43	123
<i>Alchemilla arvensis</i>	2,720	1,868	1,213	4,431	100	69	45	163
<i>Aethusa cynapium</i>	36	22	15	14	100	61	42	39
<i>Medicago lupulina</i>	99	57	34	153	100	58	34	155
<i>Sonchus arvensis</i>	54	25	7	7	100	46	13	13
<i>Galium aparine</i>	228	69	28	69	100	30	12	30
<i>G. tricornis</i>	16	4	2	7	100	25	13	44
<i>Alopecurus agrestis</i>	6,562	1,253	342	3,723	100	19	5	57
<i>Myosotis arvensis</i>	349	60	34	145	100	17	10	42

continued to flower and seed until they matured or were cut down by frost. This category includes *Anagallis*, *Atriplex*, *Bartsia*, *Euphorbia*, *Matricaria*, *Polygonum aviculare* and *Veronica buxbaumii*. Another set of species apparently increased their seed stocks by the germination and rapid development of some of their shed seeds which were lying sufficiently near the surface. *Arenaria*, *Capsella*, *Poa annua*, *Senecio* and *Stellaria* will all germinate and flower freely in the early autumn, and *Veronica hederæfolia* flowers and fruits abundantly in the very early part of the year. In all these cases the increase of seed in the soil was so large that fallowing operations from March to August failed to reduce them to their level at the previous harvest time. *Legousia* is more difficult to explain, as it has usually finished fruiting by July, and growing plants are seldom seen among the stubble. Normally, however, it germinates early, and possibly if the optimum period for germination had passed by the time of the first ploughing, practically all the seeds might have remained dormant in the soil until their favourable growing season again came round.

Proof of such occasional behaviour has already been reported in the case of *Alchemilla* (Brenchley and Warington, 1930, p. 247).

The remainder of the weed species were reduced by fallowing to a greater or less degree in spite of the delay in ploughing. This does not necessarily imply that none of these species continued to ripen seed, but rather that any increase thus effected was less than the reduction by after-cultivation. *Alopecurus*, *Papaver*, and *Sonchus*, however, are species which would be unable to increase their seed stocks to any extent during the resting time before ploughing owing to their habit of growth. All have a long vegetative period before flowering, and when a crop of seed has ripened, another year elapses before the next generation has reached the same stage, so that the delay in ploughing would not affect the efficiency of the first year's fallow with these species. The varying response of the weed species to delayed ploughing is thus not connected with the general abundance or scarcity of any particular species, but is obviously associated with habit. It happens that *Alopecurus* and *Papaver*, which together provided 87 per cent. of the total seed flora, are both species which have a long growing period before they flower and ripen seed in the summer, while *Alchemilla* and *Veronica arvensis*, which contributed a further 8 per cent., are also late-flowering species which are practically over by harvest time. In the remaining twenty-four species, contributing only 5 per cent. to the total, the increase or decrease in seed population during the season 1927-8 fluctuated as much in the scarcer species as in the more abundant (Table II).

Table II. *Relative prevalence of weed species*

Area 14 sq. ft.		
	Number of seeds in 1927	Percentage of total seeds
Papaver + Alopecurus	45,640	87
Alchemilla + Veronica arvensis	3,924	8
24 other species	2,743	5

The importance of promptitude in beginning operations after harvest is further illustrated by grouping the various weed species according to their relative seed populations after one year under fallow, and comparing the results of immediate and delayed ploughing.

Table III. *Summary of effect of fallowing for one year on percentage of weed seeds relative to number originally present in soil*

	Fallowed 1925-6 (ploughed autumn)	Fallowed 1927-8 (ploughed spring)
Over 100 %	4 species (105-136 %)	13 species (108-777 %)
81-100 %	—	4 "
41-80 %	8 "	7 "
40 % and under	16 "	4 "

Not only was the general degree of reduction much less in the 1927-8 fallow, but nearly half the species were definitely increased, whereas this only occurred with a very few species in the earlier fallow.

### III. BEHAVIOUR OF WEED FLORA WHEN LAND WAS CROPPED AFTER FALLOWING

The first crop of wheat after the two- or four-year fallow was heavy and considerably above the normal on all plots, the increase being attributed to the extra fertility accumulated during the fallow period. This initial improvement was not maintained, but the second and succeeding crops reverted to a lower level determined by the seasonal conditions. This is shown in Table IV, which gives the successive crops up to the time that another system of periodical fallowing was begun on the different sections of the field.

Table IV. *Average wheat crop on the seven plots used in the weed-seed experiment*

	Bushels of grain per acre	
	Top part of field (sections 1 and 2)	Bottom part of field (sections 4 and 5)
1925	15.4	15.6
1926	F.	5.3
1927	F.	15.5
1928	<b>49.5</b>	F.
1929	21.3	F.
1930	8.4	<b>30.8</b>
1931	F.	19.3
1932	F.	14.2

F. = fallow. Figures in heavy type show first crop after fallow.

#### (a) *Influence of first year's crop after fallow on weed flora*

It would naturally be expected that the heavy wheat crop would so dominate the situation that its competition would prevent the weed flora from reasserting itself to any considerable degree during the first year. As the wheat crop is determined in bushels of grain, which might be translated into the number of seeds produced per acre, so, too, the weed crop may fairly be estimated by the number of living seeds found in the soil at the end of the growing season. With many species the number of these seeds showed either little change or a relatively small increase or decrease by the end of the first year's cropping. The species may be arranged in three groups, according to their general response to the new conditions. In the first group *Aethusa*, *Anagallis*, *Atriplex*, *Caucalis*, *Galium tricornne*, *Sonchus* (Fig. 1) and *Polygonum aviculare* (Fig. 2) behaved very similarly after both periods of fallowing, all being species which had been reduced to very small numbers, and which remained at a low level. *Euphorbia*, *Linaria*, *Matricaria* and *Papaver* (Fig. 2) showed more variation in their behaviour, any increase or decrease not being coincident in the two series. Here again the numbers after fallow were low, with the exception of *Papaver*, which was by far the most abundant throughout. It is easy to understand the failure of species to overcome the competition of the heavy wheat crop when only a few seeds were available for the purpose,

but it is more surprising that *Papaver*, with its large stock of seed that survived the fallowing, should not have been able to re-establish itself to a greater

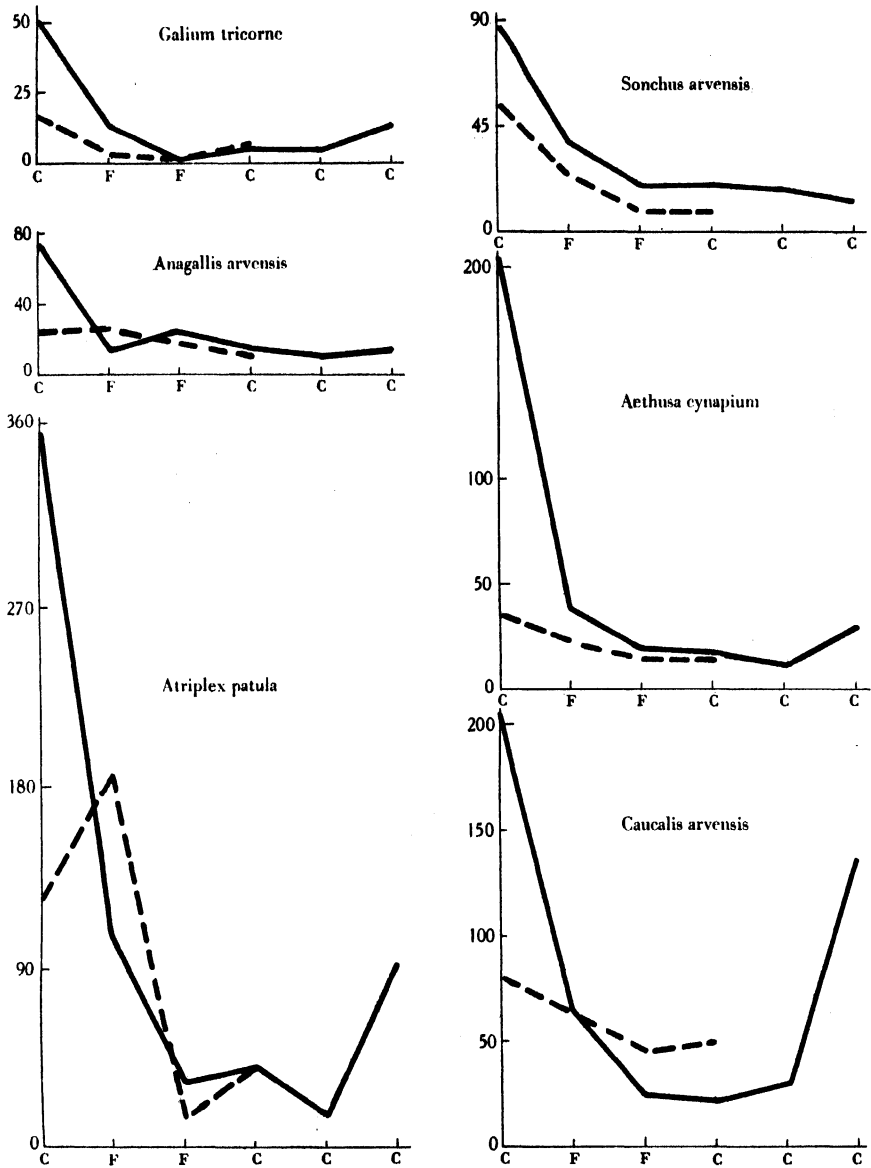


FIG. 1. Number of seedlings in 14 sq. ft. (seven plots together), fallowed —, 1925-7; - - - - 1927-9; C, land cropped; F, land fallowed.

extent. This, however, is probably correlated with the fact that *Papaver* is not at all prevalent on the heavy land in this district and so may be constitutionally less able to re-establish itself as rapidly as other species.

A second group of weeds proved their ability to withstand the competition of the wheat and had replenished their stores in the soil to a very considerable

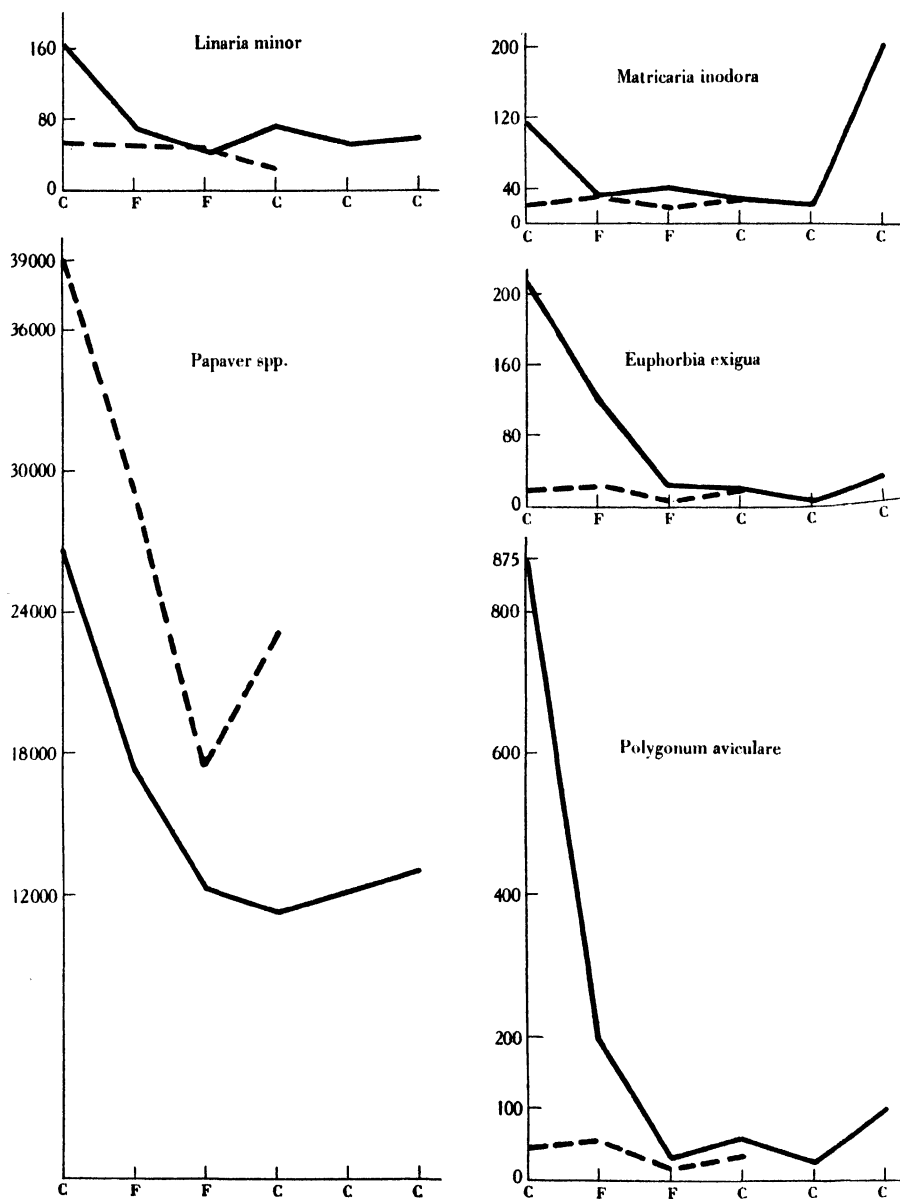


FIG. 2. Number of seedlings in 14 sq. ft. (seven plots together). fallowed ———, 1925-7; • - - - - 1927-9; C, land cropped; F, land fallowed.

extent by the time the first crop was harvested. *Alopecurus*, *Capsella*, *Myosotis* and *Veronica hederifolia* (Fig. 3) showed definite increases, though the



numbers did not always reach those present before fallowing began. *Alchemilla*, *Bartsia*, Grass spp., *Stellaria* and *Veronica arvensis* (Fig. 4) showed heavier

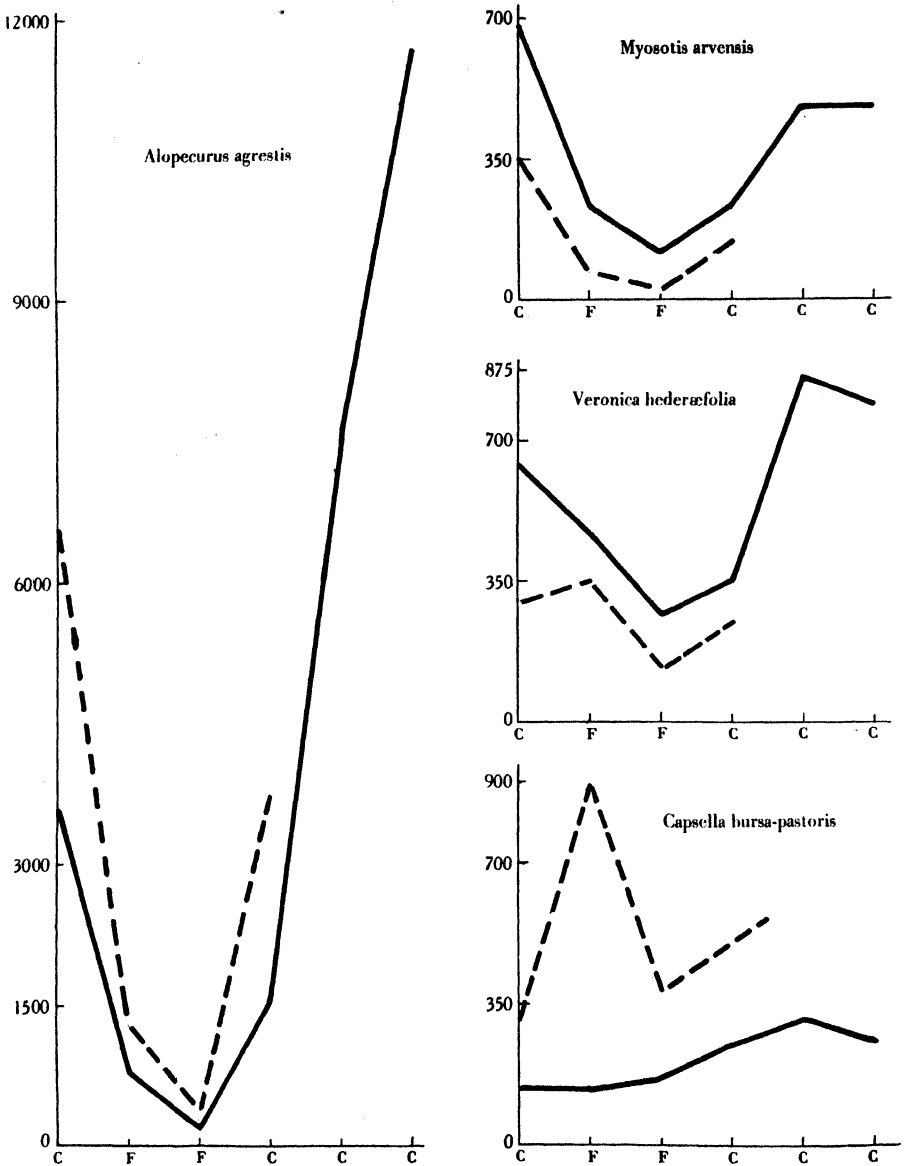


FIG. 3. Number of seedlings in 14 sq. ft. (seven plots together). fallowed —, 1925-7; - - - - - 1927-9; C, land cropped; F, land fallowed.

proportionate increases, considerably exceeding the original number before the fallow in the first three species. In all these the response was similar after

both periods of fallow. With most of them, the habit of the weeds may account for their success. *Capsella* and Grass spp. (chiefly *Poa annua*) can flower and

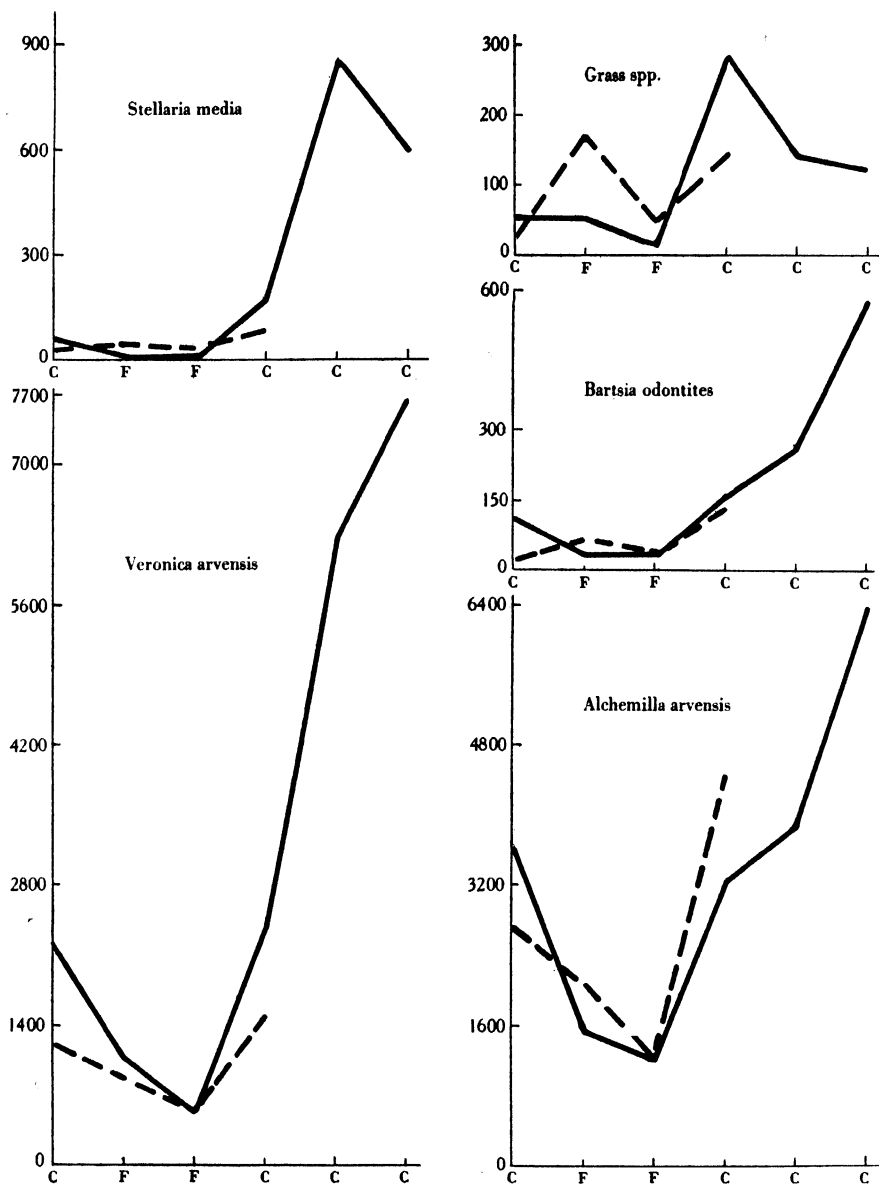


FIG. 4. Number of seedlings in 14 sq. ft. (seven plots together). fallowed ———, 1925-7; - - - - - 1927-9; C, land cropped; F, land fallowed.

seed all the year round, and so would be able to restock the soil with seed during the autumn and winter months when the growth of the wheat was as yet

insufficient to bring it into effective competition. *Alchemilla*, *Myosotis*, *Stellaria*, *Veronica arvensis* and *V. hederæfolia* are all species in which the

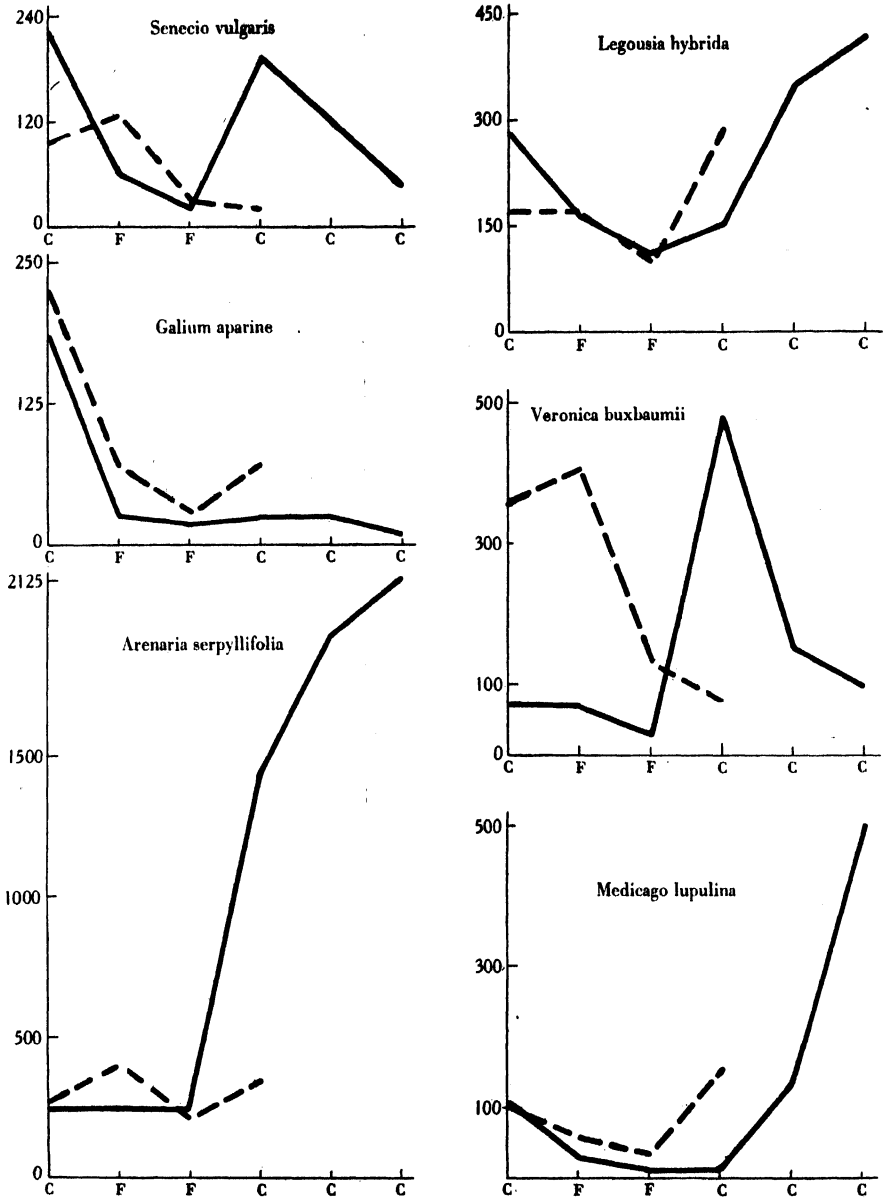


FIG. 5. Number of seedlings in 14 sq. ft. (seven plots together). fallowed ———, 1925-7; ----- 1927-9; C, land cropped; F, land fallowed.

earlier flowers ripen seed long before the plant reaches maturity, and here again seed formation had probably begun before the wheat competition came

much into action. *Alopecurus* is the only late-flowering upright species in this group, and its success is probably due to the fact that its habit of growth is closely parallel to that of the wheat. Crop and weed germinate and grow up together, flowering at much the same time, and sufficient *Alopecurus* plants must have developed from the relatively small stock of seed left after fallowing to lay the foundation for a rapid recolonisation.

In a third group are the species whose response to cropping varied more widely after the two fallow periods. *Arenaria*, *Senecio* and *Veronica buxbaumii* (Fig. 5) showed heavy increases after the 1925-7 fallow, but *Arenaria* rose only very slightly after the 1927-9 period, while the other two species diminished in number. On the contrary, *Galium aparine*, *Legousia* and *Medicago* (Fig. 5) improved their position more after the second fallow than after the first. It is not possible to suggest a reason for the divergent behaviour of these species, though it was probably connected with the seasonal conditions that occurred at critical times in development.

(b) *Prevalence of weed species in second and subsequent years after fallowing*

To a great extent the behaviour of the various weed species during the first year after fallow was continued for the next two years. Most species which failed to reassert themselves during the first year remained at a low level afterwards, whereas the majority of those which had shown a distinct upward tendency continued to increase more or less considerably, this behaviour being independent of the actual proportion of any species in the total population. The weeds may be classified in groups according to their response during the three years after fallow (cf. Table I and Figs. 1-5).

(1) Little or no recovery throughout: *Aethusa*, *Anagallis*, *Euphorbia*, *Galium aparine*, *G. tricornis*, *Linaria*, *Papaver*, *Sonchus*.

(2) Little or no recovery in first two years, then an increase: *Atriplex*, *Caucalis*, *Matricaria*, *Polygonum aviculare*, *Scandix*.

(3) Increase in first two years, then fall or steady in third: *Capsella*, *Myosotis*, *Stellaria*, *Veronica hederifolia*.

(4) Steady increase throughout: *Alchemilla*, *Alopecurus*, *Arenaria*, *Bartsia*, *Legousia*, *Medicago*, *Veronica arvensis*.

(5) Quite irregular in behaviour: Grass spp., *Senecio*, *Veronica buxbaumii*.

This grouping applies to the response after the 1925-7 fallow for which exact data are available, and the indications from field observations after the later fallows are that on the whole the general trend of behaviour of the various species is similar.

*Papaver* and *Galium aparine* showed a greater early increase, and *Arenaria* a less marked recovery in the first year after the 1927-9 fallow, which may have influenced their later response to some extent.

The varying rate of recolonisation has resulted in a definite change in the balance of the weed flora, as some previously plentiful species have now become relatively insignificant, while others have come into much greater prominence. The persisting reduction of *Papaver* is the dominant feature in this change of balance, as the numbers are so large as to mask the more rapid increase of the rest. The steady reduction in the total seeds present in the soil caused by fallowing was followed by an equally steady increase year by year.

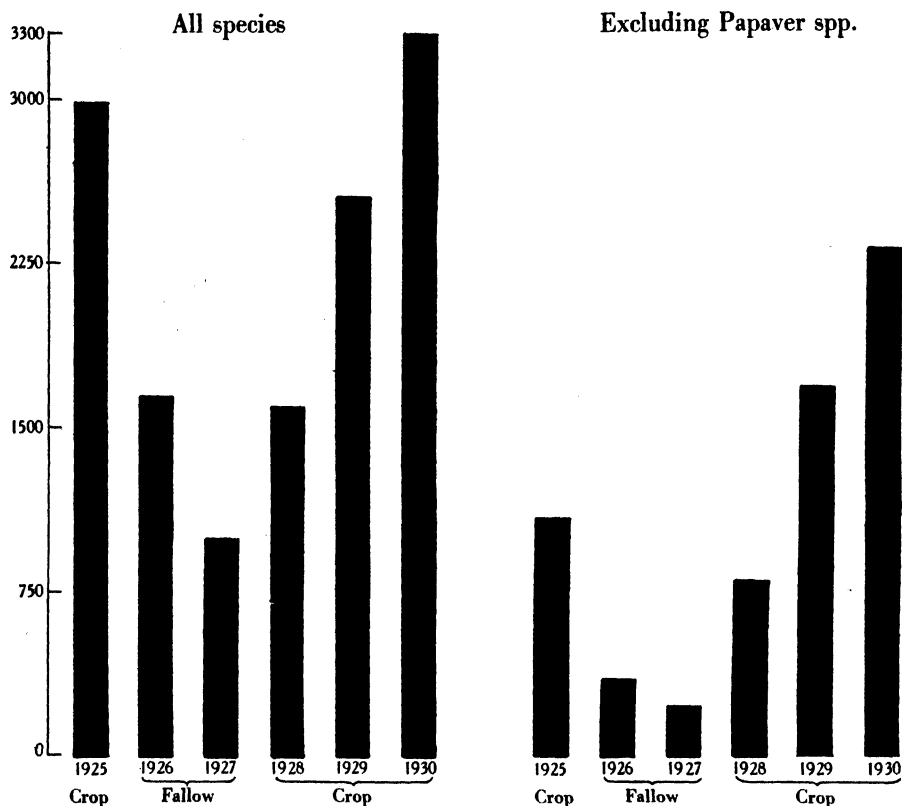


FIG. 6. Average number of weed seeds per sq. ft. (seven plots together), showing re-establishment of weeds during the first three years after fallowing.

After the third wheat crop the total number of buried weed seeds had reached and slightly exceeded the number present at the time fallowing operations began. From this point of view the beneficial effects of fallowing persisted for two years. Leaving *Papaver* out of consideration, however, the recolonisation by all other species was much more rapid. After the first crop the number of weed seeds had closely approached, and after the second crop far exceeded, the original stock present before fallow, the rise being continued in the succeeding year (Fig. 6). This rapid increase in weed seeds coincided with a parallel decrease in the yield of wheat, but no opinion can be expressed as to

how far the relative movements of crop and weeds were correlated, especially as reduction in crop did not induce a corresponding rise in *Papaver*. As regards weed reduction, however, fallowing is for most species only a temporary expedient. There is also a certain risk that some species may profit by the after-fallow conditions to such an extent that their increase may be so rapid as to make them a serious menace after the lapse of a very few years. The critical period seems to be the behaviour during the first year of return into crop, when the future line of development of most species is apparently determined.

Fallowing operations were primarily intended to reduce *Papaver* and *Alopecurus*, and were successful for *Papaver*, but the return of *Alopecurus* was unduly rapid. This is well shown in Fig. 7 which illustrates from left to right



FIG. 7. Second crop of weeds from samples taken after harvest in 1929. Left to right: 16 3 A, after four years under fallow; 16 4 A, after two years under fallow; 16 2 C, after two years in crop, following two years under fallow.

the scarcity of seedlings after four and two years fallow, and the abundance of *Alopecurus*, with other species, after two years in crop following two years fallow. The sample in each case represents only one quarter of a square foot of soil in area. The competition factor of *Alopecurus* has always been considered to be high, and a detailed comparison of crop yield and the number of *Alopecurus* seeds was made to see how far the two species reacted on one another. Complete data were available between 1925 and 1933 for seventy-seven cases in which wheat followed wheat on the various sections of the seven plots under examination. In fifty-five of these cases, as the wheat yield increased, the number of *Alopecurus* seeds decreased, and *vice versa*, but in the remaining twenty-two instances the crop yield and *Alopecurus* seeds moved in the same direction, both increasing or decreasing simultaneously. It would, therefore, seem that while the two species usually come into active competition, conditions frequently occur which supersede the competition factor and either

encourage or discourage wheat and *Alopecurus* alike. A few random instances may be quoted (Table V) to show that the divergence of the figures is quite outside the bounds of experimental error and also that the necessary conditions cannot be seasonal, as the yields of *Alopecurus* and wheat may run both parallel and in opposition on different parts of the same plot in the same year.

Table V. *Increase or decrease of yields of wheat and Alopecurus*

Plot	Section	Year	Running parallel		Plot	Section	Year	Running in opposition	
			Crop Bushels of grain per acre	<i>Alopecurus</i> No. of seeds per sq. ft.				Crop Bushels of grain per acre	<i>Alopecurus</i> No. of seeds per sq. ft.
5	5	1926	2.2	190	5	5	1925	7.7	123
		1927	6.5	255			1926	2.2	190
		1930	34.6	593			1930	38.9	39
7	4	1931	20.2	375	7	3	1931	27.0	117
		1929	22.9	955			1929	22.9	596
		1930	6.4	852			1930	9.7	1836
12	1	1929	26.3	1251	12	2	1929	26.3	635
		1930	6.0	924			1930	9.9	1767
		1925	14.2	614			1926	3.6	400
16	2	1926	3.6	273	16	1	1927	15.3	243
18	4	1925			18	5	1926		
		1926					1927		

(c) *Effect of prolonged fallowing upon the subsequent weed flora*

So far no account has been given of the section of Broadbalk field which was left uncropped from 1925 to 1929, the cultivation during this period being identical with that of the area under a two-year fallow in the same year. The response of the crop was similar after both long and short fallows, heavy yields being obtained in the first year, followed by a considerable drop in the second. The average yields of grain on adjacent sections of the seven experimental plots were as follows:

	After 4 years fallow (bushels per acre)	After 2 years fallow (bushels per acre)
1930	39.0	36.3
1931	22.6	21.8
1932	17.7	15.2
1933	26.2	25.6

The competition offered by the crop to the weeds was, therefore, very much the same in both sections, and it will be seen later that the weed response was also very parallel.

The check in weed seed reduction due to delayed cultivation in 1927-8 described on p. 481 was also shown in the course of the long fallow. Species that were able to increase their number before the delayed fallowing operations were begun, were equally able to do so where the land had already been under fallow for two years and no fresh seeds were available. A comparison of Table I with Table VI shows clearly the parallel behaviour of the majority of the species concerned. The species for 1928 in Table VI which show a definite

increase after two years fallow, correspond almost exactly with those for the same year in Table I where fallowing was only beginning.

Table VI. *Number of viable weed seeds on area fallowed for four successive years (all seven plots together)*

	Crop		Fallow		Crop	
	1925	1926	1927	1928	1929	1930
Grass sp. (chiefly <i>Poa annua</i> )	26	32	9	<b>90</b>	50	233
<i>Bartsia odontites</i>	18	15	10	5	10	26
<i>Capella bursa-pastoris</i>	80	109	60	<b>229</b>	64	119
<i>Senecio vulgaris</i>	150	45	8	<b>106</b>	53	40
<i>Arenaria serpyllifolia</i>	138	156	111	<b>154</b>	100	186
<i>Atriplex patula</i>	95	24	21	14	3	13
<i>Stellaria media</i>	42	6	1	<b>57</b>	64	252
<i>Matricaria inodora</i>	11	34	4	<b>9</b>	2	6
<i>Polygonum aviculare</i>	258	89	15	<b>20</b>	—	21
<i>Veronica hederaefolia</i>	268	239	111	109	37	57
<i>V. buxbaumii</i>	44	54	23	<b>113</b>	45	42
<i>Euphorbia exigua</i>	101	53	11	6	—	4
<i>Anagallis arvensis</i>	21	7	3	<b>5</b>	2	1
<i>Legousia hybrida</i>	278	158	140	84	58	199
<i>Linaria minor</i>	36	34	9	9	1	6
<i>Scandix pecten</i>	223	34	3	<b>4</b>	—	—
<i>Caucalis arvensis</i>	68	37	17	<b>22</b>	6	4
<i>Polygonum convolvulus</i>	18	5	1	—	—	—
<i>Papaver</i> spp.	18,001	10,959	8,280	6,063	3,760	5,319
<i>Veronica arvensis</i>	1,045	472	198	137	103	279
<i>Alechemilla arvensis</i>	1,980	942	622	532	269	1,002
<i>Aethusa cynapium</i>	77	31	4	<b>5</b>	2	5
<i>Medicago lupulina</i>	47	15	2	<b>4</b>	8	1
<i>Sonchus arvensis</i>	38	8	4	<b>8</b>	3	3
<i>Galium aparine</i>	56	8	5	—	—	—
<i>G. tricornae</i>	16	7	5	—	1	—
<i>Alopecurus agrestis</i>	1,809	437	87	<b>93</b>	29	624
<i>Myosotis arvensis</i>	90	51	19	12	7	28

Figures in heavy type indicate increase in seed population after delayed cultivation of fallow. The species are arranged in the same order as in Table I to facilitate comparison.

With few exceptions the numbers increased, decreased or remained stationary after the first year's return into crop, regardless of the length of the previous fallowing. *Scandix*, *Galium aparine*, *Galium tricornae* and *Polygonum convolvulus* appeared to be eliminated by the long fallow as not a single seedling appeared. *P. aviculare*, on the other hand, increased apparently from nothing after the long fallow, indicating a rapid increase from a residual stock of seed which was so small that no representative appeared in the samples taken in the last uncropped year. *Medicago* and *Linaria* were the only species that varied strikingly in behaviour with the different periods of fallowing. Both remained in fair quantity at the end of the two years fallowing period, and under the first crop *Medicago* was multiplied several times whereas *Linaria* was further decreased. The longer fallow reduced them both far more heavily, but the ultimate behaviour was reversed, as *Linaria* improved its position while *Medicago* became still less plentiful. This depression with *Medicago* continued with the second wheat crop in 1931, and it was not till 1932 that



it began to make any progress, though it still remained much behind that on the area that had been under short fallow. Figures for this later period are available for three plots, on only one of which (plot 18) *Medicago* occurs in any appreciable amount.

Table VII. *Behaviour of Medicago lupulina after long and short fallows*

	Last year of fallow 1929	Crop		
		1930	1931	1932
Long fallow, 4 years	1	—	1	47
Short fallow, 2 years	4	16	45	108

Generally speaking, therefore, the ultimate behaviour of most weed species is not affected by the length of time the land is repeatedly cultivated under fallow, as in most cases the increase or decrease under crop is identical in direction. When the cultivations are carried out at the right time to check any species from producing fresh seed, the population is reduced more heavily with a longer period of fallow, and it takes longer for any particular species to regain its original position. It must be realised, however, that under normal farming conditions such prolonged fallowing is impracticable, the usual period being one year or less, but in the present instance the weedy condition of the experimental wheat field demanded special treatment, thus providing a unique opportunity for investigating the question of the behaviour of seeds present in the soil.

#### IV. OBSERVATIONS ON PERIODICITY OF GERMINATION AND LENGTH OF NATURAL DORMANCY OF BURIED WEED SEEDS

In the first paper of this series a distinction was drawn between the "natural" and "induced" dormancy of seeds. A seed may be said to be naturally dormant if it will not start into growth when it is placed in conditions favourable to germination, whereas "induced" dormancy is that state forced on a seed when it is capable of immediate germination but finds itself in circumstances that are unfavourable to growth, as when seeds are buried too deeply, or soil conditions are too arid. The aim of fallowing operations is to prevent induced dormancy and to bring as many buried seeds as possible to the surface where they can germinate if they are ready. In the laboratory experiment the fallowing conditions are intensified, as the soil is disturbed regularly and frequently and favourable growth conditions are maintained throughout. In spite of this many seeds have remained inert in the seed pans for several years. More than fifty of the total samples taken in 1925, 1926 and 1927 were retained after the normal three-years period, and these have since been treated exactly the same as more recent samples and are still under observation. Altogether an additional 1610 seedlings have appeared,

representing twenty-one species, of which five have only contributed one or two individuals. The proportion of these later seedlings to the total number of germinated seeds is shown in Table VIII.

Table VIII. *Prolonged natural dormancy*

Species	Total No. of seeds recorded from samples	Viable seeds remaining dormant for more than 3 years		Longest period of dormancy recorded till Dec. 31st, 1935 Years
		No.	%	
<i>Aethusa cynapium</i>	126	41	32.5	10
<i>Anagallis arvensis</i>	91	44	48.4	10
<i>Medicago lupulina</i>	231	75	32.5	10
<i>Polygonum aviculare</i>	323	18	5.6	10
<i>Arenaria serpyllifolia</i>	437	68	15.6	9
<i>Bartsia odontites</i>	39	14	35.9	9
<i>Euphorbia exigua</i>	133	23	39.8	9
Grass spp.	44	2	4.5	8
<i>Papaver</i> spp.	39,389	1,182	3.0	8
<i>Alchemilla arvensis</i>	3,979	50	1.3	7
<i>Capsella bursa pastoris</i>	250	14	5.6	7
<i>Polygonum convolvulus</i>	19	2	10.5	7
<i>Alopecurus agrestis</i>	4,998	1	0.02	5
<i>Atriplex patula</i>	259	18	6.9	5
<i>Galium tricornue</i>	17	3	17.6	5
<i>Scandix pecten</i>	222	3	1.4	5
<i>Stellaria media</i>	49	1	2.0	5
<i>Veronica arvensis</i>	2,202	40	1.8	5
<i>Caucalis arvensis</i>	130	5	3.8	4
<i>Myosotis arvensis</i>	324	4	1.2	4
<i>Sonchus arvensis</i>	81	2	2.5	4
		1,610		

*Aethusa*, *Anagallis* and *Medicago* have appeared steadily up to date, showing that they can have a period of natural dormancy of at least ten years. *Polygonum aviculare* produced a single seedling in 1935, after an interval of four years. This is noted for its prolonged dormancy, as it was the most abundant species which appeared on Geescroft Field at Rothamsted on land which had been under grass for thirty years (Brenchley, 1918). The remaining species show a maximum dormant period of four to nine years, though it is quite possible that some viable seeds are still present.

Most of the species retaining their vitality longest are those in which the largest *proportion* show prolonged dormancy, irrespective of the *number* of seedlings produced. The only exceptions are *Polygonum aviculare*, which experience has shown to be most erratic in its germination, and *P. convolvulus* and *Galium tricornue*, of which so few seeds occurred altogether that a single belated seedling represented a large increase in the percentage in the proportion surviving for more than three years after sampling. The high proportion of prolonged dormancy in the first two groups (Table VIII, excluding *Polygonum aviculare*) is noteworthy, and may afford some explanation of the abrupt seasonal changes in the abundance of the species, as the population in any one year is not necessarily dependent upon successful seeding in the

immediately preceding year, but may result from long-buried seeds becoming capable of germination and causing an unexpected influx of a particular species.

Under field conditions where fallowing is carried on for a limited time and the soil is also disturbed less regularly, the proportion of viable seed that reaches the surface in a given time may be less than in the shallow pans used for germination. Consequently many buried seeds which have passed out of their period of natural dormancy may perforce remain in a condition of induced dormancy, ready to spring up among the crops at a later date when cultivation eventually brings them to the surface. Species which produce many seeds that remain naturally dormant over long periods form an incalculable element in the weed flora. It is impossible to forecast their behaviour, for periods of great abundance of a particular species may be followed by times of great scarcity or even absence, after which it may again reappear in greater or less amount. The factors determining this behaviour are unknown and render such temperamental weeds, of which *Polygonum aviculare* is an excellent example, peculiarly difficult to deal with under field conditions. After eleven years' work it is now feasible to confirm or modify the opinions expressed in an earlier paper (Brenchley and Warrington, 1930, pp. 246-60) with regard to periodicity of germination and the length of possible dormancy in the weed species concerned. In most cases the original suggestions have been to a large extent corroborated by the later work. The majority of species which showed steady decrease in the numbers germinating annually in the first set of samples behaved similarly in the later sets, while those showing irregular periodicity usually repeated this behaviour, though the direction of irregularity frequently varied. With *P. aviculare* the extreme irregularity of germination was confirmed, but the suggestion of a possible two-year period of natural dormancy was not borne out, as a certain proportion survived for ten years. The variation in behaviour of the two species of *Galium* proved constant. *Galium aparine* repeatedly behaved normally with a steady annual decrease in germination in each sample, and a period of dormancy not exceeding three years, whereas *G. tricornis* was irregular in periodicity, and showed a relatively large proportion of seeds with longer dormancy, up to a five years limit to date. *Aethusa* and *Euphorbia* confirmed the forecast, both being of very irregular germination and coming high in the scale of dormancy, both as regards time and number.

Some species which occasionally germinate in a normal, regular manner may usually be irregular in their behaviour, as *Anagallis*, *Atriplex* and *Medicago*, all of which were regular in 1925 samples, but generally irregular since. With *Anagallis* and *Atriplex* the suggestions have been confirmed, *Anagallis* giving a high proportion of seeds remaining dormant over a long period, while *Atriplex* has a relatively short dormancy.

*Medicago* is a most temperamental weed, and has entirely failed to come up to expectations. Instead of having a short dormancy as originally suggested,

it has proved to have one of the longest, with a very high proportion of seeds germinating after the third year. In fact, *Medicago* with 32.5 per cent. and a ten-year period is second only to *Anagallis* with 48.4 per cent. and a similar ten-year period. On the other hand, on some occasions, as 1932, a large proportion of the seeds were in such a hurry to germinate that the seedlings appeared thickly in the pans within two days of the samples being washed out and set up. A similar behaviour is sometimes noticed in the field on a wet stubble, when the ground may be carpeted with *Medicago* seedlings long before the land

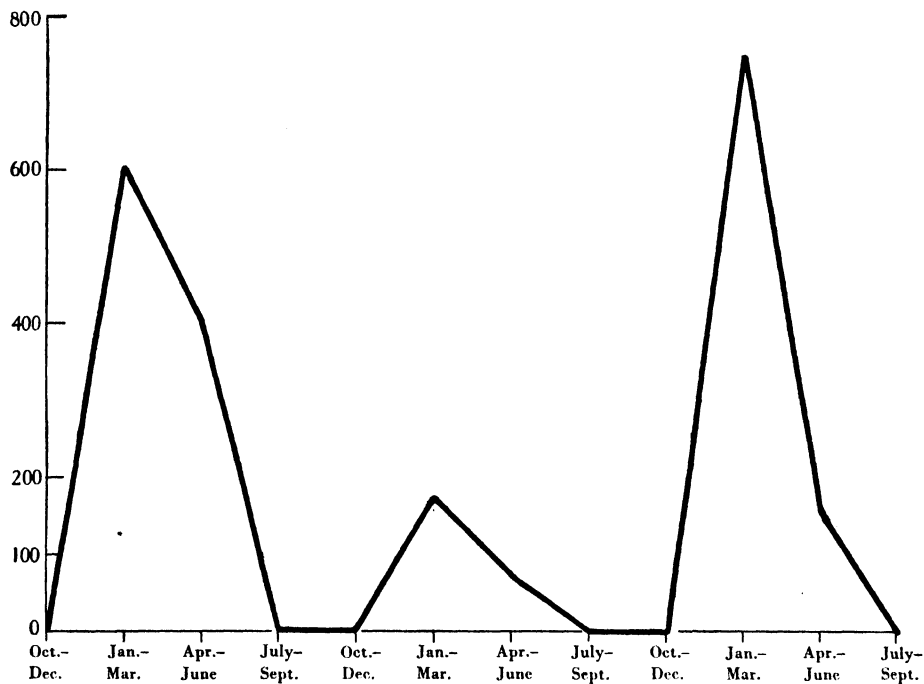


FIG. 8. Total number of seedlings of *Bartsia odontites* from all samples taken from 1925 to 1935, graphed according to season of germination.

is ploughed. The conditions which cause this behaviour are not clear. It is not merely a question of an abundant water supply, as, if it were, this premature germination should occur every year in the sample pans, whereas it is rarely seen there. It is probably some combination of climatic conditions during the ripening of the seeds which brings them to such a state of maturity that they are ready to germinate immediately an adequate water supply is available, no further period of after-ripening being necessary.

*Caucalis* has continued to show regularity in germination, but the indicated long dormancy has not been confirmed. On the contrary, the proportion of seeds lasting for four years has been quite low, and no later records have appeared. This result is unexpected and somewhat surprising, as in the field

*Caucalis* is very seasonal, which was originally attributed to prolonged dormancy. It is possible, however, that the breaking of dormancy in *Caucalis* may be dependent on environmental conditions, and that in the field it may be forced to lie dormant for a longer period owing to unfavourable circumstances.

*Bartsia* exhibits more spectacular behaviour than any other species, and the original note needs considerable modification. Germination is very irregular; for instance, high figures may be obtained in the first and third years, with low figures in the second. Dormancy is much longer than was anticipated, running on to nine years instead of the suggested two years. Periodicity of germination is very strongly marked, as with only four exceptions all the seedlings appeared in the first six months of the year (Fig. 8). None came up in January and very few in June, the period of germination thus being practically confined to February–May, which is well illustrated by the samples taken in 1930 (Table IX).

Table IX. *Germination of Bartsia odontites, over three-year period*

Sample taken 1930	
December–January	0
February–March	584
April–May	148
June	18

In view of the parasitic nature of *Bartsia*, this raises the interesting question as to whether the restricted germination period has been developed in correlation with the time that the gramineous hosts of the species are in the most suitable condition for attack and whether, too, there is any question of heredity in the time of germination of particular individuals or species.

#### V. ABNORMALITIES IN SEEDLING DEVELOPMENT

Since 1925, during the course of this experiment, 1140 soil samples have been dealt with from Broadbalk field. Altogether 641,171 seeds of various species were handled and identified to December 31st, 1935, of which 378,605 were *Papaver* spp. (Table X). With figures of this magnitude it was to be expected that certain abnormal seedlings would occasionally appear. Apart from a few injured or malformed plantlets the only true abnormalities noticed were albinos and seedlings with three or four cotyledons.

The albinos were confined to two species, *Alopecurus agrestis* and *Papaver rhoeas*, and were very scarce (Table XI).

The proportion of albinism in the grass was relatively much greater than in the dicotyledonous poppy, and this provides an interesting confirmation of casual observations extending over many years. In dealing with large numbers of seedlings of various species in experimental work at Rothamsted albino seedlings of cereals and grasses have been noticed from time to time, whereas albino dicotyledons were rare, though very occasionally an albino *Pisum sativum* occurred.

Table X. *Total number of seedlings obtained between November 13th, 1925 and December 31st, 1935 from 1140 samples, totalling 285 sq. ft. in area  $\times$  6 in. deep*

Papaver rhoeas	378,605	Sonecio vulgaris	1,888
Alopecurus agrestis	81,498	Atriplex patula	1,786
Alchemilla arvensis	76,766	Scandix pecten	1,464
Veronica arvensis	38,869	Caucalis arvensis	1,308
Arenaria serpyllifolia	10,327	Linaria minor	1,106
Veronica hederæfolia	8,851	Galium aparine	1,118
Capsella bursa-pastoris	5,583	Euphorbia exigua	1,016
Legousia hybrida	5,343	Matricaria inodora	883
Myosotis arvensis	4,717	Aethusa cynapium	761
Stellaria media	4,543	Sonchus arvensis	503
Veronica buxbaumii	3,137	Anagallis arvensis	363
Medicago lupulina	3,337	Galium tricornu	197
Polygonum aviculare	2,580	Polygonum convolvulus	168
Bartsia odontites	2,168	16 species, each below 100	294
Grass spp. (chiefly Poa annua)	1,992		
Total excluding Papaver		262,566	
Total including Papaver		641,171	

Table XI. *Occurrence of albino seedlings*

	No. of albinos	Total No. of seedlings	Proportion of albinos
Alopecurus agrestis	21	81,498	1 : 3,881
Papaver rhoeas	6	378,605	1 : 63,101

*Tricotyledonous seedlings* appeared in small numbers throughout the experiment, and a solitary *Papaver* was found with four cotyledons. In these abnormalities the replications appear to be confined to the cotyledons, for there is only a single central bud as in a normal seedling. The total number of seedlings available in many species was sufficiently large for examples of tricotyledony to be expected to occur if this phenomenon was at all characteristic (cf. Table X). Nevertheless it appeared in only seven species, the proportion varying considerably, ranging from 1 : 984 in *Veronica hederæfolia* to 1 : 19,435 in *V. arvensis* (Table XII). It is interesting that the highest and

Table XII. *Occurrence of tricotyledonous seedlings*

	No. of seedlings with three cotyledons	Total No. of seedlings	Proportion of tricotyledons
Papaver spp.	94	378,605	1 : 4,028
Alchemilla arvensis	28	76,766	1 : 2,742
Veronica hederæfolia	9	8,851	1 : 984
<i>V. arvensis</i>	2	38,869	1 : 19,435
Capsella bursa-pastoris	1	5,583	1 : 5,583
Bartsia odontites	1	2,168	1 : 2,168
Caucalis arvensis	1	1,308	1 : 1,308

lowest proportion of tricotyledony should fall within the same genus, while no instances were observed in a third species *V. buxbaumii*, of which 3068 seedlings occurred.

Considering all species together, the number with three cotyledons was very low, only 136 out of a total of 641,171 on Broadbalk field, showing a ratio of 1 : 4714, confined to seven species of which two belonged to the genus *Veronica*.

In this connection reference may be made to *Spergula arvensis*, the dominant weed in a parallel experiment on sandy soil from Woburn, where five seedlings out of a total of 35,430 showed tricotyledony, giving a proportion of 1 : 7086.

## VI. SUMMARY

1. Delay in cultivation after harvest prevents the reduction of various weeds by fallowing. Some species, already developed, continue to ripen seeds, and others have time to germinate and reach the seeding stage before they are cut down by cultivation. The numbers of extra seeds thus produced may be greater than those destroyed by fallowing, so that the reducing effect of the operation is entirely nullified.

2. When land is recropped after fallowing the first wheat crop tends to be abnormally heavy, thus introducing increased competition with the weeds. Some species fail to reassert themselves, but others are able to withstand the competition of the wheat and can replenish their stores of seed in the soil by the time the first crop is harvested. A few species vary in their response, either remaining at a low level or re-establishing themselves quickly after fallowing.

3. Species which soon begin to reassert themselves tend to increase rapidly in number and after three years under crop they may be much more plentiful than they were before fallowing began, *Alopecurus agrestis* and *Stellaria media* being notable examples. Other species tend to remain at a low level, and the varying rate of re-establishment results in a definite change in the balance of the weed flora. Though *Papaver rhoeas* was only reduced to about half its original number by fallowing, it has failed to increase to any great extent, so that it is no longer the dominant feature that it was before fallowing was begun.

4. Prolonged fallowing, for four years, reduces the store of buried weed seeds more drastically, but does not eliminate them all. The ultimate re-establishment of species follows the same lines as after a shorter period of fallow, though it takes longer for any species to regain its original numbers of viable seeds in the soil.

5. The period of natural dormancy of most species on Broadbalk proved to range from four to nine years, but four species may prove to be able to lie dormant for more than ten years.

6. *Bartsia odontites* showed very strongly marked periodicity of germination, as every seedling appeared between February and June, the majority appearing early in the year.

7. Relatively few abnormal seedlings have been observed in over 600,000 which germinated. A few albinos occurred in *Alopecurus agrestis* and *Papaver rhoeas*, and also a certain number of tricotyledonous seedlings belonging to seven species, chiefly *Papaver* spp., *Alchemilla arvensis* and *Veronica hederifolia*.

## REFERENCES

- Brenchley, W. E. and Warington, K.** "The weed seed population of arable soil. I. Numerical estimation of viable seeds and observations on their natural dormancy." *This JOURNAL*, **18**, 235-72, 1930.
- Brenchley, W. E. and Warington, K.** "The weed seed population of arable soil. II. Influence of crop, soil, and methods of cultivation upon the relative abundance of viable seeds." *This JOURNAL*, **21**, 103-27, 1933.
- Brenchley, W. E.** "Buried weed seeds." *J. Agric. Sci.* **9**, 1-31, 1918.



## CORRESPONDENCE

### EAST AFRICAN VEGETATION TYPES

To the Editor of *The Journal of Ecology*.

SIR,

I am not an ecologist, but as a student of geography, watching, describing and attempting to explain vegetational *change* wherever it comes my way, I have naturally tried to take the results of ecological science for a guide. I must, however, confess that thus far this hoped for guidance has not proved very successful, largely, I believe, owing to the great diversity of definitions which the various schools of ecology apply to their nomenclature. On the other hand, when travelling and working among natural and man-altered vegetations, I find it of the greatest importance, and not, as a rule, very difficult, to establish by direct observation of facts a correlation of most vegetation types with the *local* climate, soil, water-supply and man's disturbing activities. And I consider it more useful for an eventual understanding of nature's constant "flux"—certainly from the point of view of geographical synthesis—to rely on such observable facts rather than on preconceived theories put into the form of "probable", and therefore problematical, succession charts.

When, therefore, my old friend and co-worker in East Africa, Prof. John Phillips, published his important papers<sup>1</sup> on parts of Tanganyika Territory whose geography I have studied for many years, I thought the elaboration of a few of my field notes might be helpful to an ecologist even when coming from a layman.

As Phillips, to whom I had sent my little manuscript, has given me the satisfaction not only of finding my notes worthy of discussion in his recent "Analysis of Concepts",<sup>2</sup> but of calling them "provocative", I feel, not without considerable hesitation, that a greater number of ecologists might be interested in reading them. I do so more particularly as Phillips appears to have misunderstood me entirely when, on p. 232, he states that I "require a climatically uniform region for development", and that I "hold that unchanging climatic conditions are essential to development of the climax". I "require" and "hold" of course nothing of the sort! My text (in which I use "development" in its everyday sense) makes it perfectly clear, I think, that, on the contrary, my arguments and conclusions are *conditional* on the orthodox Clements-Phillipsian definitions into which, as I am trying to prove, my observed facts simply do not fit.

I am therefore now submitting my original Notes of December 1931 for publication without alterations except for two short additions marked as such.

#### SOME NOTES ON THE DANGERS OF ECOLOGICAL STUDIES UNCHECKED BY CO-ORDINATION WITH THE RESULTS OF OTHER SCIENCES

I cannot, do not, dare not wish to be dogmatic on "succession", that very great and useful and, one may add, sometimes abused conception of modern ecology; especially not where statements or suggestions are concerned emanating from such high authority on African ecology as Prof. J. Phillips. As a geographer, however, who looks upon the phytogeographical complex from a ~~less~~ narrow angle than the pure ecologist and who must draw into his considerations the morphological features (in both their static and their dynamic aspect), as well as their influence on the regional distribution of climatic and edaphic

<sup>1</sup> "Some important vegetation communities in the Central Province of Tanganyika Territory." *S. Afr. J. Sci.* **26**, 332-72, 1929 (republished in *This JOURNAL*, **18**, 1930, 193-234), and "The floral regions of Tanganyika Territory," *Trans. Roy. Soc. S. Afr.* **19**, 363-72, 1931.

<sup>2</sup> *This JOURNAL*, **22**, 554-71, 1934; **23**, 210-46, 488-508, 1935.

differences, I may be permitted to raise my voice against some of the generalisations contained in Prof. Phillips's recent paper on "The floral regions of Tanganyika Territory" (*Trans. Roy. Soc. S. Afr.* 19, 363-72).

First of all I must warn against the too exclusive importance attributed to fire in East African successional studies. For although every one with his eyes open will readily agree that no consideration of East African vegetation types and their successions can afford to neglect the influence of fire, one can not, in my opinion, make fire the supreme "leitmotiv" for the development of climax vegetations as the author apparently does (p. 372).

Much more serious, however, is Prof. Phillips's arrangement of his major climatic regions, which, from the geographer's point of view, does not do justice to a complicated dovetailing of greatly differing climatic types over vast areas of the territory, a dovetailing whose pattern is given by the present-day orographical forms, themselves the expression of geologically very recent and, for aught we know, still continuing tectonic happenings.

I shall here only deal with the largest of the author's regions, the Great Central Plateau (pp. 371-2), for the many different vegetation types of which he arrives at the tentative conclusion that they all develop towards the "Deciduous Scrub" (his type VII) as the climax vegetation. My argument against this generalisation is as follows: If, as I understand the concept, succession means the development of vegetation types within a *climatically uniform* region, and if by climax we define the final stage of the mutually dependent development of vegetation *plus* soil under *unchanging climatic conditions*, then we cannot possibly fit into one and the same successional series two vegetation types (be they climax types or not!) which, like the East African "Deciduous Scrub" and the "*Berlinia-Brachystegia* Woodland (or Miombo)", are, I maintain, the typical representatives of two very markedly differing climates. As far as our still very scant observations, especially with regard to evaporation and to "effective rainfall" as opposed to actual precipitation, allow us to do so, we can draw a rough boundary between these two climate types at the Isonotide depicting a "rain-factor" of 40, which separates a distinctly subarid from a definitely more humid (the so-called "savannah") climate. Now, it is the main point of my argument that in the great tectonic "shatter-belts" of East Central Africa the differential uplift of a large number of individual crust blocks, frequently if not everywhere accompanied by a westerly tilt, i.e. a tilt *away* from the moisture-laden trade winds, has resulted in a complicated orographical rearrangement of a formerly more uniform peneplain surface. Over vast areas of the "Central Plateau" (between the Great Scarp in the east and the Central African (Tanganyikan) Rift Valley in the west) high and low change frequently and rapidly; east-facing scarp slopes exposed to the prevailing trade winds alternate with west-facing dip-slopes lying in more or less pronounced "rain-shadow"; and large basins of interior drainage form subarid or even arid islands in the vast expanses of the more humid, tectonically undisturbed (or less disturbed) uplifted plateau peneplains.

This very varied topography dictates equally varied climate and is, to my mind at least, the direct cause of the present-day distribution of the two major vegetation types within Prof. Phillip's "plateau Region". It is thus misleading to look upon this region as one of uniform climate, and all successional attempts based on such assumed uniformity are consequently bound to arrive at erroneous conclusions.

On the other hand, if we accept the orographical and climatic pattern described above and continue our successional studies separately for each of the two types (better still if, with advancing knowledge, we can arrive at a further subdivision) we shall not only be in a position to work out our purely ecological problems much more satisfactorily, but shall be able to study the economically most important question whether or not the East African climate as a whole tends to become more humid or more arid; whether such a tendency can be expressed by cycles; whether it is helped or hindered by the activities of man, among which his fires probably occupy the front rank.

For if we can establish definite proof that in a certain area "Scrub" is gaining on "Miombo" or *vice versa* we shall no longer be mistakenly led to see therein proof for a certain successional direction, but rather for climatic change which interrupts the smooth progress of succession under heretofore uniform climatic conditions.

Personally I do not know of any definitely established instance of such gaining of one vegetation type on the other; but Prof. Phillips has himself recorded (1929, p. 353) the gaining of Scrub on Miombo in an area of interior drainage where a gradual spreading of aridity on to the higher slopes is what the geographer would naturally expect. On the other hand, I know of many instances where the *sudden* change, often without even the narrowest marginal zone of transition, from typical Baobab Scrub to typical Miombo can be easily and immediately co-ordinated with the orographical features (generally primarily influencing exposure) and this not only regionally but also with regard to the most intricate detail of the minor forms and changes of topography.

To sum up: *Whether or not Miombo or (and) Deciduous Scrub are the climax forms of their respective climates I must leave to the decision of the ecologist. But I maintain—and I do not know of any observations to the contrary—that Miombo and Scrub are expressions of very different climatic conditions and that, as such, they cannot be members of the same successional series.*

(Added in 1935: I am aware that the last words may be, and have been misconstrued by ecologists. What I meant to convey indirectly when writing them is my doubt, which is, I believe, justifiable, whether, in view of the observed facts, the whole idea of primary succession leading to a monoclimate—or postclimate—is applicable to the parts of East Central Africa here discussed.)

If the foregoing is an example of how the pattern of differing climates within a region can and does affect successional studies, I shall discuss in the following an example of an "edaphic pattern" within a region of undoubtedly uniform climate which likewise, when overlooked, must lead to entirely wrong conclusions with regard to successional stages. The vegetation forms concerned are, again, "*Berlinia-Brachystegia* Woodland" or "Miombo" and that very curious form of Scrub described by Prof. Phillips as "*Grewia*- other spp. Scrub" or "Itigi Thicket", his type VI of the plateau communities (*op. cit.* p. 372), for which in his previous paper (*op. cit.* pp. 218-19 and Chart, p. 222) he works out a probable succession from Miombo to thicket.

The area concerned is the southern and central part of the Kilimatinde-Turu High-Block which, in the east, drops in stepped fault-blocks into the dischargeless Bubu Low-Block, and in the west descends by more gentle slopes into the Wembere Depression. Geologically this block consists essentially of Granite which is covered extensively by a fairly thick formation of "Duricrust" (to use Woolnough's very descriptive expression), very probably the result of pleistocene (?) peneplain conditions of drainage. On the as yet untouched, gently rolling peneplain of the plateau itself this crust is interrupted here and there by higher remnant hills and ridges of the former erosive cycle which now rise from the level crust country as granite islands. On the stepped scarps in the east the scarp slopes expose the faulted granite, while the surfaces of the steps generally tilted slightly westward, still carry remnants of the crust, especially on their higher, outer edges. And a vigorous back-cutting of the scarp, as well as of the Wembere drainage, is actually eroding a network of valleys through the duricrust into the underlying granite. Recent tectonic movements and the sculpturing forces set free by them are thus responsible for an intricate pattern of the two rocks (granite and duricrust), for the study of which the cuttings of the Central Railway between Makatupora in the Bubu Plain and Kazikazi on the Plateau, and those of the newly built branch line to Singida offer excellent opportunities. The road from Manyoni to Kilimatinde likewise leads through very instructive exposures, and the air survey recently undertaken by Mr Burt of the Tsetse Research Department, with the object of demarcating

the extent of the Itigi Thicket, will, when its results have been co-ordinated with the ground topography, provide further admirable material for the study of this pattern. Now, whatever the physical and chemical properties of the soils derived from the granite and from the duricrust, there can be no doubt that the two are very different in character, so that the tectonically and morphologically determined pattern of rock distribution becomes automatically an "edaphic pattern" with regard to the plant communities it nourishes; and field observations invariably show that the, more often than not, very sudden change from Thicket to Miombo always coincides with a change from duricrust soil to granitic soil. Here the additional fact must be mentioned that, as a rule, the slopes in the duricrust peneplain are very gentle, while granite generally crops out on the steeper slopes of the younger erosive cycle. This fact undoubtedly influences the subsurface water conditions, and may, together with the more strictly edaphic conditions of soil, prove a determining factor for the plant communities.

Climatically the region covered by Itigi Thicket on duricrust, and by Miombo on granite, is, as Prof. Phillips remarks, uniform. Between approximately 950 and 1350 m. above sea-level both the scarp face and the level plateau, very gently inclined westward, have practically the same exposure and therefore the same humidity. The lowest 100 m. or so of the scarp, however, which lie below, i.e. outside, the beneficial influence of the belt of increased condensation, participate in the markedly more arid climate of the Bubu depression and therefore carry neither Miombo nor Itigi, the place of both formations being taken by the normal deciduous thorny scrub characteristic of this climatic type and reacting but little, if at all, as is well known, to edaphic differences. The result is that, below 950 m., granite and duricrust are no longer separators of plant communities.

Phillips' "relict-stands" of Miombo (*op. cit.* p. 218) are thus clearly proved to be edaphically determined, and are far from indicating a succession from Miombo towards a thicket climax. On the contrary, if one studies the problem dynamically, one finds definite proof for a gradual but continuous displacing of the thicket by encroaching Miombo; a displacement which, if one adheres to the strict definition of succession as something taking place under uniform outer conditions, cannot be called succession at all. It is, rather, the result of a very distinct change of soil conditions due, in this case, to purely tectonic causes and their morphological consequences. Already a number of localities on the Saranda Scarp are known, and the aerial survey mentioned above will, it is believed, add more such localities, where we can watch back-cutting erosion denude the duricrust and lay open the underlying granite, where the change from the clayey yellow eluvial soil of the former to the more sandy granitic soils can be observed and measured, and where, following the change of soil, Miombo visibly pushes back the Thicket.

To sum up: *Miombo and Itigi Thicket are plant communities whose distribution over a climatically uniform region depends on that of originally differing soils and therefore cannot be brought into the same successional series.*

(Added in 1935: References to the soils mentioned are based on field observations only. The Amani Pedologist has, however, quite recently collected material for a closer study of the differences of these soils which, it is hoped, will shed additional light on the ecological problem.)

Yours faithfully,

C. GILLMAN.

## REVIEWS

### THE JOURNAL OF ANIMAL ECOLOGY

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THE spring number contains ten papers, reviews of thirteen publications, and 141 notices of publications on animal ecology. In addition, the reports of the Annual Meeting, accounts, address list of members and new rules, are reproduced from *The Journal of Ecology*, a practice which will be continued in future. A duplicate set of the notices is issued in a form suitable for indexing.

A long and important paper representing a whole life's work, by A. E. Boycott, reviews exhaustively the distribution and ecology of British freshwater Molluscs and contains a large bibliography. This paper was published by the Society as a special supplement. The other nine papers are all of a rather solid and serious nature, being concerned mainly with fact-finding rather than theory. An exception is a population study by the Russian workers G. F. Gause, N. P. Smaragdova and A. A. Witt, who used both mites and Protozoa as experimental material for determining the interaction of predators and prey. The results of this work are subjected to a penetrating mathematical analysis. Maud J. Norris' (Mrs O. W. Richards) measurements of the fertility of *Trogoderma versicolor*, a beetle sometimes found in stored products; Taskhir Ahmad's very complete determination of the biotic potential of the flour-moth *Ephestia kuehniella* under different conditions; and P. A. Buxton's discussion of the seasonal breeding rhythms of rats in the tropics, are all important contributions to the ecology of animal populations. John R. Baker describes a useful "nomogram" for working out saturation deficiencies from various figures ordinarily available. Field surveys include Carmel F. Humphries' comprehensive study of the deeper bottom and littoral communities of Windermere by means of quantitative sampling methods; James H. Fraser's survey of zonation among rock pool Copepoda on the shores of the Isle of Man; and Gwion Davies's account of the numbers and distribution of badger colonies around Denbigh. H. D. Slack gives analyses of the food of Caddis fly larvae (which were mainly found to be herbivorous).

Reviews include *The Journal of Ecology*, February issue; a full summary of recent German work on the Chinese mitten-crab's spread in Europe; recent marine and estuarine community studies in the United States and England; the periodical *Zoogeographica*; and works on plant ecology, human ecology, migration of animals, porcupines, land planning, the regional survey of Hitchin, and the fauna of Palestine.

CHARLES ELTON.

**Stapledon, R. G.** *The Land Now and To-morrow*. Pp. xvii and 336, with numerous photographs and 2 maps. London: Faber and Faber, Ltd. Price 15s.

This book deals with "land utilisation from a national point of view", taking into account "not only the relation of a prosperous countryside—which includes agriculture, forestry and rural industries—to the national well-being, but also providing facilities in the country and amidst truly rural surroundings for the recreation and relaxation of the urban population". This is an immense topic, but Prof. Stapledon is able to face it with wide and deep knowledge and experience. His first thesis—and one that will be generally admitted—is that the land itself is one of the nation's greatest heritages; and the land itself, he insists, is of more importance than what it grows. This may seem perverse to the narrow utilitarian, but it is in profound accord with one of the deepest and soundest of human instincts. Prof. Stapledon's feeling for the land is inborn in most, if not in all of us, but in him it has been developed

and enriched by continuous occupation on the land and with the problems of the land, while in the townsman the land feeling is starved and often perverted.

It is easy to show that we have misused and are misusing this most concrete of our national heritages: it is much more important to point the way to improvement, and this Prof. Stapledon is able to do in a thoroughly well documented and for the most part wholly convincing exposition of the complex problems involved and their proper solutions. He never takes a narrow or one-side view, but considers all legitimate uses to which the country may be put—hunting, shooting, riding, walking, motoring, bicycling, golf courses and playing fields, as well as forestry, pasturage and tillage. And it is this broad touch with country life in all its aspects that makes the book so satisfying as well as so fascinating. One of the most attractive chapters is devoted to the design for a National Park, in the area round Plynlymon, ideally one of many in the country at large. Here provision could be made for country recreation in its widest sense, with a full equipment of camping grounds, hostels and the like, while at the same time the productive life of the area was developed so that the holiday maker would be brought into the closest touch with sheep-rearing, the natural industry of the region.

The overwhelmingly pastoral character of British agriculture is seen from the fact that nearly two-thirds of the whole area of Great Britain is under "permanent grass" or "rough grazings", while arable contributes not much more than a fifth and woods and plantations only a twentieth. "Grass" then, and the flesh into which it is transformed, are very much the most important products of our soil. Prof. Stapledon's two main practical theses are first that "permanent grass"—much of which is in fact derelict, semi-derelict or extremely unproductive—is a wasteful and unremunerative form of pasture, and secondly, that the "rough grazings" can be enormously improved. The former should be largely if not wholly replaced by "long leys" sown with pedigree grasses and clovers, while the latter require different treatments, various combinations of cultivation, manuring, sowing with specially bred strains, and regulated grazing. It is in this last field that Prof. Stapledon's own work and that of his staff at Aberystwyth have already led to results that appear almost miraculous, as anyone who inspects the Cahn Hill Improvement Scheme near the Devil's Bridge can see for himself. On the one hand the skilled geneticists of the Welsh Plant Breeding Station have produced and are producing strains of the standard pasture grasses and clovers which are far better fitted for their purpose than the ordinary commercial strains; and on the other the ingenious cultivation, manuring and sowing with these improved strains, of hill grasslands which were almost worthless, is demonstrating the possibility of turning them into sound profit-earning pastures, supporting immensely increased flocks. These brilliant results, which may be literally epoch-making for the pastoral industry, are due to the combination of scientific work in the greenhouse and on the experimental plot with the practical knowledge which comes from long years of experience on the land, from tireless ingenuity and persistence, and from the constant readiness to learn from failures and successes alike.

To the ecologist the book, and still more a personal visit to Aberystwyth, will be of great value from several points of view. In the first place it illustrates the ways in which the most important "biotic factor", namely grazing, actually works. Just as the famous park grassland experiments at Rothamsted demonstrated that you could completely alter the composition of grassland by differential manuring alone, so the work at Aberystwyth shows that you can completely alter it by differential grazing alone; though it is the combination of the two, with initial cultivation and sowing of the most suitable strains, that gives the best and most profitable results. Secondly, it brings into relief the very different reactions of different genetic strains of the same species to environmental conditions. Thirdly, it provides, or can provide, really detailed and solid knowledge of the autecology of different species and different strains. And finally, to sum up the whole, it prevents the over-emphasis of single factors, making abundantly clear that it is the interaction of many different factors which produces the results we see in the field.

*The Land Now and To-morrow* has had an enthusiastic Press, and is selling extremely well. It is cheering to learn of the increasing number of enquiries from farmers and landowners as to how they may best apply the results of the Aberystwyth work to their own land. We may therefore look forward with some confidence to the results of Prof. Stapledon's work, in combination with the modern recognition of the supreme feeding value of *young grass* and the greatly improved methods of drying hay now available, leading to a very considerable advance if not a complete transformation, in our pastoral industry, with the best effects on the prosperity of the countryside and national well-being.

In regard to the larger aspects of the author's topic, perhaps it is too much to hope that we shall get a statesman who will look beyond the temporary palliatives of marketing schemes and regulations, and will consider the future of the land, as Prof. Stapledon does, in terms of its best use by the people as a whole. If it is not done soon it will be too late, for to-day we are travelling with increasing rapidity towards the complete alienation of the land from its proper uses.

A. G. T.

**Clarke, G. R.** *The Study of the Soil in the Field*. Pp. 142, with 7 figures in the text. Oxford, at the Clarendon Press, 1936. Price 5s.

This little book is devoted to an aspect of soil science which is rightly coming to be regarded as fundamental, viz. the study of *natural soils in the field*. The time is happily past when chemical and mechanical analysis of samples brought to the laboratory was held to be the beginning and end of the subject. The author is well known for his skill in observing and interpreting soil profiles in the field, and, though it is possible to criticise his exposition in some points of detail and arrangement, there is no doubt that Mr Clarke's knowledge and experience will render this description of field methods substantially useful to all concerned with the practical scientific study of the soil.

A. G. T.







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